The Canadian Entomologist

Vol. LXXXVI Ottawa, Canada, December 1954 No. 12

The Light Reactions of Larvae of the Spotless Fall Webworm, *Hyphantria textor* Harr. (Lepidoptera: Arctiidae)[1]

By W. G. Wellington[2], C. R. Sullivan[3] and W. R. Henson[4]

Recently, the light reactions of three species of tent caterpillars were described (3). The present paper contains a similar description of the responses of larvae of the spotless fall webworm, *Hyphantria textor* Harr. This species was chosen for comparative study because, like tent caterpillars, it is colonial through most of its larval stage, during which it forms extensive webs.

Larvae of all six instars were studied. Some of the behaviour described here was first observed during the summers of 1949-50 at Sault Ste. Marie, Ont. During July and August of 1953, several of the laboratory tests were repeated at Sault Ste. Marie, and, in addition, some new reactions were observed for the first time.

MATERIALS AND METHODS

All the larvae used were field-collected during their first or second instars. Several colonies were placed on hazel (*Corylus* sp.) in the field and allowed to complete their development with as little interference as possible. They were observed closely each day to obtain information on their light reactions under natural conditions.

Larvae required for laboratory tests were reared on *Salix* sp. indoors throughout their developmental period. The rearing room was kept between 20-21°C. and 50-55% R. H. At first, these larvae were reared in Fiske trays, but development was slow, because younger larvae consistently webbed their food before beginning to feed, and the leaves in the trays dried too much while they were being webbed. Therefore, in subsequent rearings, larvae were kept in 6-cm. Jars and given only a few leaves each day, so that the time spent in spinning silk was not excessive.

Laboratory experiments included light-board tests of responses to a six-watt panel lamp at room temperature, and observations of the effects of higher temperatures on the responses to overhead light in a dark-light alternative chamber. The rearing room temperature and humidity ranges were used to acclimate larvae before both types of tests, and no additional acclimation level was employed.

The alternative chamber differed slightly from the one previously described (3). It was constructed by G. W. Green, and was based on an earlier design of his (1) that had a completely transparent lid, so that an observer could see the movements of insects on both the dark and light parts of the platform. The present model retained this feature and was heated from below as usual, but the light source was placed above the chamber, as in the past, instead of being combined with the heat source underneath, as in Green's original apparatus (1). Consequently, it was possible to shut off the heat without interfering with the light. Light was blocked from any part of the platform by an

1Contribution No. 181, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.
2Forest Biology Laboratory, Victoria, B.C.
3Forest Insect Laboratory, Sault Ste. Marie, Ont.
4Forest Biology Laboratory, Calgary, Alta.

adjustable mask clamped below the lamp. The mask was mounted far enough above the lid of the chamber so that an observer could see the whole platform. As in previous work, water was used to keep the air in the chamber moist.

As a rule, individual larvae were observed during tests on the light board, and groups were used in the alternative chamber. In the chamber, larvae were distributed at random on the platform in groups of five to ten, depending on their size, and were allowed to form their initial aggregations before the chamber temperature was raised. The reaction range of a group was determined by recording the temperature at which each insect finally modified or reversed the sign of its reaction, and then noting the two extreme temperatures at which this occurred in each group. In addition to these group tests, movements of individuals in the chamber were observed during one part of the work, since it was found that group results could not always be interpreted until some additional information on the actions of individuals was collected.

RESULTS

Reactions to a Point Source

Examples of typical reactions of larvae to the small six-watt panel lamp at moderate temperatures are shown in Figs. 1 and 2. Fig. 1 shows the types of paths obtained from fed and starved larvae. Larvae of the first two instars

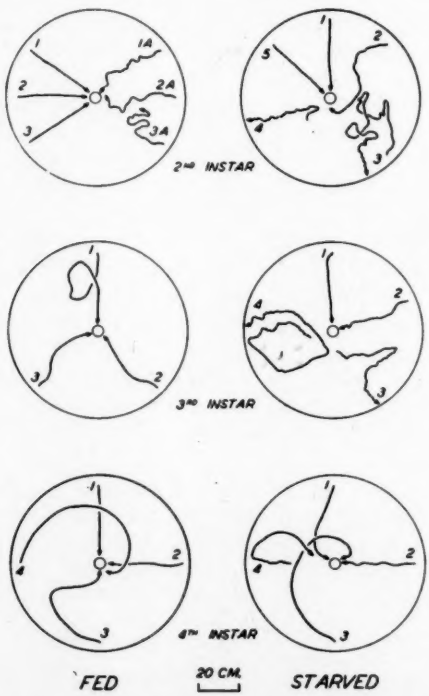

Fig. 1. Tracks of fed and starved *Hyphantria* larvae of instars II-IV in response to a six-watt panel lamp. In the diagram for fed second-instar larvae, tracks 1-3 were made by larvae that had been warmed to 24-25°C on the light board. Tracks 1A-3A in this diagram, and all tracks in the other diagrams, were made at 20-21°C. In all diagrams but that for fed second-instar larvae, the numbers on the tracks refer to consecutive trials.

behaved similarly, so the second-instar tracks shown in the first two diagrams of the figure serve as examples of both.

Fed first- and second-instar larvae were tested immediately after removal from foliage on which they were observed feeding (i.e., no larva was selected unless it was actively feeding). At temperatures below 24°C., they moved sluggishly and their orientation was inaccurate, as shown in the series of tracks labelled 1A-3A in the first diagram. When the light board was warmed to 24-25°C. beforehand, however, their movement to the lamp was not only more rapid, but also more direct, as shown in tracks 1-3 in the diagram.

When the larvae were starved for 24 hours, it was no longer necessary to warm the board to obtain a rapid and accurate initial response to the light. The initial path to the lamp was generally similar to track 1 in the diagram for starved second-instar larvae. Subsequent trips, shown as tracks 2-5 of that diagram, were less predictable. The second trip generally produced a more devious track similar to that shown in track 2. The path followed during the third or fourth trips always contained a part in which the larva travelled directly away from the light, either temporarily, as in track 3, or consistently, as in track 4. There was never any doubt that the larva was still making use of the light source during these apparently photonegative movements, because its head was continually thrown backwards, with violent swings from side to side, in the characteristic manner of a photonegative animal. We have endeavoured to show this on the tracks by drawing these portions in a closely spaced zigzag pattern.

Such behaviour might persist during numerous later tests, but frequently an apparently photonegative individual would suddenly revert to the type of track shown as number 5 of the series, and maintain this heading for five or six additional tests, after which it would once again produce the types of paths shown in tracks 3 and 4. More prolonged starvation produced no more consistency.

Larvae of subsequent instars did not require a warmed reaction platform, whether they were fed or starved. Paths followed during consecutive tests are shown for larvae of the third and fourth instars in the remaining diagrams of Fig. 1. Tracks of *fed* larvae of the third and later instars were very similar. It will be seen that fourth-instar larvae soon began to approach the light indirectly even when they were fully fed. Since similar behaviour also was noted in fed larvae of the fifth and sixth instars, their tracks are not shown.

On the other hand, when larvae of the last four instars were starved for 24 hours, differences in behaviour appeared. In the third instar, more consistent movement from the light than that exhibited during earlier instars soon appeared, generally during the third or fourth trial, as shown in the diagram. During more prolonged starvation, many larvae continued to follow paths much like that shown in track 3 (third instar, starved). Sometimes, an indivdual reacted as shown in track 4, however, and remained in this state throughout subsequent starvation.

In track 4, the larva appeared to be responding to the light source continuously, but apparently confined its movements to a zone bounded by definite light intensities. The track illustrated has been distorted for easier viewing, but in reality, later sections followed the original sides closely, but not exactly (i.e., there was no tendency to follow a silk trail). On each "photonegative leg", the larva moved slowly, constantly throwing back its head in the direction of the lamp. Each time it reached a point about 35 cm. from the lamp (3.7 foot-candles), it began to turn, speeding up considerably as it turned towards

the lamp, and reducing the amplitude of its head swings. It never travelled directly towards the lamp, however, and never approached closer than about 10 cm. (30 foot-candles) before turning away again.

As noted, larvae of the fourth and later instars soon began to move indirectly towards the light whether they were fed or starved. Movement away from the light occasionally occurred because of disturbance, but there was never any consistent pattern to it, and truly photonegative behaviour did not occur in older larvae before their period of prepupational travel. The only consistent difference noted between fed and starved larvae of these instars was that fed larvae occasionally reverted to direct trips to the lamp during later tests of a series, whereas those that were starved for 24 hours or more never went directly to the light unless they were treated as described below.

Some years ago it was reported that starved, photonegative larvae of the tortricid, *Choristoneura fumiferana* (Clem.), could be made to revert to photopositive behaviour by treating them in various ways, particularly by ligaturing them around the fifth segment of the body (4). As long as the ligature remained in place, or did not become too loose, the insect responded photopositively. When the ligature was loosened or removed, the insect immediately responded photonegatively. Since these observations, each species we have subjected to light tests has been checked for comparable behaviour, without results until the present time. When starved mature larvae of the spotless fall webworm were tested, it was found that they too could be induced to change to a rigidly photopositive response. An example is shown in Fig. 2

Fig. 2 shows six consecutive trials of a sixth-instar webworm that had moulted two days before the test, and had been starved for 24 hours just prior to the test. Best results with this and other individuals were obtained by ligaturing around segment VI of the body, although reactions were sometimes obtained when the thread lay at an angle across both segments V and VI. Ligaturing other segments did not produce a change in response.

Sixth-instar larvae of *H. textor* are large enough so that, with a little practice, an observer can remove a ligature and replace it several times without using any anaesthetic to quiet the insect. This was done with the individual that made tracks shown in Fig. 2.

In Fig. 2, the first three tracks show the paths during three preliminary consecutive trials before the insect was ligatured. These tracks show a consistent type of reaction. After test 3, a loop of thread was pulled tight enough around segment VI so that the body, which felt slightly flaccid after starvation, firmed appreciably. The loop was left loose enough, however, for the animal to crawl without interference, and the knot was placed on the dorsal surface so that the ends did not drag and influence the direction of travel. The larva was tested immediately, and the resulting path is shown in track 4.

As soon as the larva reached the lamp, the thread was removed and the insect was returned to the starting zone. Track 5 was obtained, after which the ligature was immediately replaced. The subsequent trial produced track 6. Attempts to remove the ligature again resulted in injury, so the tests were stopped. As noted previously, starved larvae of this instar never went directly to the light unless treated in this manner.

The day before pupation, sixth-instar larvae feed very little, but they are active, and sometimes move directly away from the lamp when tested. Ligaturing a larva in this state invariably produced an indirect approach to the light, but no direct approach similar to those in Fig. 2 was ever obtained.

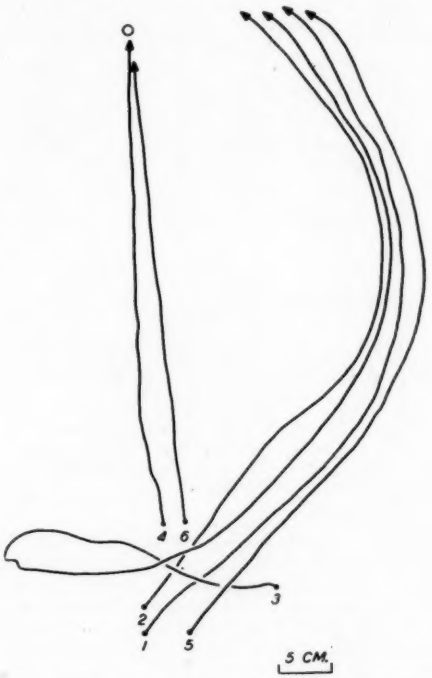

Fig. 2. Six consecutive tracks of a sixth-instar *Hyphantria* larva starved for 24 hours before being tested with a six-watt panel lamp at 20.5°C. Tracks 1-3 show the movements of the larva while it was allowed to crawl without disturbance. Before track 4, the larva was ligatured with thread around the sixth body segment. The ligature was removed at the end of the trial, so that track 5 was made while the larva was free. The ligature was replaced for track 6.

During the last half-day before pupation, the larvae do not feed at all, but they are then too sluggish to test.

Reactions to Overhead Light

During tests of the effects of high temperatures on these reactions, observations of groups had to be discontinued temporarily while the behaviour of individuals at moderate and high temperatures was clarified. Without such detailed observations, it was impossible to obtain consistent values for the ranges of the reaction temperatures for the instars. Two distinct types of responses to boundaries were observed, and these are shown in Fig. 3.

The platform shown in Fig. 3 had a central spot of light surrounded by an annular shadow. When very small larvae are used, this arrangement is better than a simple division of the platform into dark and light halves, because the boundary is so close to any part of the illuminated area that small larvae may reach it before they are overheated (cf. 1). In the diagrams of the figure, the tracks of two second-instar larvae are shown, first at room temperature, and again after the temperature had been raised until both larvae were photonegative.

Diagrams A and A′ show boundary reactions typical of the majority of the insects observed. In A, the larva responded photopositively at room temperature, and seldom overshot the illuminated area. Reactions to the dark-light boundary

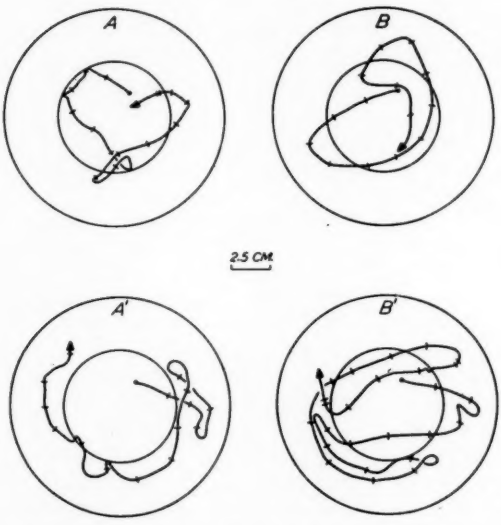

Fig. 3. Types of boundary reactions observed in a dark-light alternative chamber that contained a central spot of light surrounded by an annular shadow zone. Tracks A and B show the different responses of two second-instar *Hyphantria* larvae at room temperature. Tracks A' and B' show the responses of the same two larvae at temperatures above their photic reversal points. Tracks B-B' show overshooting characteristic of rapidly moving larvae. Time marks on the tracks indicate 10-second intervals.

were generally marked and immediate, and when the larva did overshoot into the dark, it turned quickly and moved directly back into the light. Similarly, in A′, at a temperature above its reversal temperature, the same larva exhibited the same type of boundary reaction while it was photonegative.

On the other hand, the larva shown in B and B′ seldom showed an immediate reaction at the boundary. This seemed to be partly because it moved more rapidly at all times than the larva shown in A-A′. Indeed, the small minority of larvae (about 10 per cent of those tested) that moved constantly and very rapidly about the chamber all exhibited this lack of response as they crossed the boundary, and continually overshot into the other zone, whether they were cool or warm. Examination of the periods they spent in each zone showed, however, that they were photopositive at room temperature, and photonegative above their reversal temperatures. Nevertheless, the presence of one or two of these individuals in a group of ten larvae made it very difficult to determine the reaction range of the group, because they were continually reentering the light after the upper limit of the group reversal range had been reached.

Tests of series of individuals showed that the reaction ranges of both types of larvae were similar. Consequently, in later work, when a group was first placed in the chamber, it was observed for a few minutes, and its more active members were removed and replaced by quieter individuals. This made it easier to determine the reaction range of the group.

Both fed and starved larvae were tested in the chamber, with the results shown in Table I. Once again, as in the tent-forming species of *Malacosoma* (3), it was found that fed or starved larvae of the fourth and subsequent instars were indifferent, or only weakly photopositive at lower temperatures, but very strongly

photopositive at higher temperatures. Their two types of behaviour are shown in Fig. 4, which shows the tracks of a fully-fed fourth-instar larva in the chamber.

Track A of Fig. 4 shows the path taken from the dark to the illuminated half of a chamber when the larva was at room temperature. This individual was very sluggish, and did not move for five minutes after being placed in the

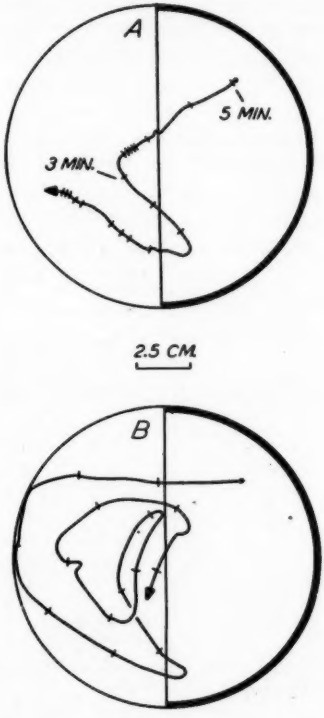

Fig. 4. Tracks of a fourth-instar *Hyphantria* larva in a dark-light alternative chamber. Track A shows the sluggish response of the larva when released in the dark half of the chamber at room temperature. Track B shows the immediate response when the larva was released in the dark half at a temperature above its photic reversal point. Time marks on the tracks indicate 10-second intervals except where minutes are shown.

dark. Time-marks at ten-second intervals show its progress thereafter, except at the point in the light where it stopped for three minutes. Despite its sluggishness, it was clearly photopositive. (It is worth noting that the larvae that were not sluggish at room temperature also spent considerable time in the dark as well as in the light.)

Track B shows the behaviour of the same larva when it was heated above its reaction temperature. Once again it was released in the dark half of the chamber, but this time it moved directly and rapidly to the light. These tracks should be compared with A and A′ in Fig. 3, so that the difference between stronger photopositive behaviour and a change to photonegative behaviour at high temperatures will be clear.

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Apart from the change in the type of response at high temperature during and after the fourth instar, additional points shown in Table I are the steady rise in reaction temperature with instar, and the marked lowering of the reaction temperature of each instar after 24 hours' starvation.

TABLE I.

Effects of Temperature on the Light Reactions of Spotless Fall Webworm Larvae in a Dark-Light Chamber
(100 Larvae per Instar. Temperatures in Centigrade)

Condition:		Fully Fed		Starved 24 hours	
Instar	Reaction change at temperatures shown	Range	50% Point	Range	50% Point
I	*P+ to P−	27.8–30.2	28.5	—	—
II	P+ to P−	29.0–31.5	30.8	26.0–29.5	28.0
III	P+ to P−	30.2–33.0	32.0	27.0–30.8	29.5
IV	weak to strong P+	31.3–34.5	33.5	28.0–32.3	31.0
V	weak to strong P+	32.3–36.2	35.0	29.5–33.5	32.0
VI (to 1½ days of pupation)	weak to strong P+	33.0–37.0	35.5	30.2–34.5	32.5
VI (within 1½ days of pupation)	indifferent or weak P+ to strong P+	(little or no feeding)		31.5–34.2	32.5

*P+, photopositive; P−, photonegative

Reactions to Light from the Sky

The observations described in this section were made outdoors at the laboratory. Previous papers (2, 5, 6, 7) have included descriptions of the effects of changes in the internal temperatures of insects on their directions of travel over the ground, and notes on their directional changes in response to changes in the plane of polarization of light from the sky. In the most recent paper (6), a new technique was described that was also used in the present work to study the movements of *Hyphantria* larvae on the ground.

A large sheet of graph paper, backed by heavy cardboard, is placed flat on the ground, preferably on a lawn or similar even surface. A pin inserted in one corner of the paper casts a shadow that can be aligned with one of the lines of the grid, so that the paper may be kept orientated with respect to the sun. A thermocouple inserted in the surface of the paper gives a measure of the temperature of the surface and its boundary-layer air, and also gives nearly instantaneous indications of changes in this composite temperature.

An insect is allowed to crawl on the paper, and its path is traced. Each time a directional change occurs, it is numbered, and the corresponding tempera-

ture reading is taken immediately. When a slow-moving insect is used, 10-30 such changes may be obtained before it reaches the edge of the paper, but rapid crawlers, such as mature larvae of *Malacosoma* and *Hyphantria*, leave the paper too quickly to be suitable experimental animals.

When a track is complete, the angle each segment forms with the grid lines indicating solar direction is measured. These angles are then plotted against their corresponding temperature readings, and the regression of orientation angle on temperature is computed. During plotting, a heading directly towards the sun is recorded as 0°, and one directly away is recorded as 180°. If simple linear regressions are to be computed, angles between 180-360° should be transferred to the 0-180° range.

Typical results are shown in Fig. 5, based on observations of the movements of a second-instar *Hyphantria* larva. In the diagram, line A shows the various headings adopted by the fully fed larva as the temperature changed. Line B shows the new headings taken by the same larva after 48 hours' starvation. In both instances, the larva was held at 20.5°C. and 50% R. H. for at least 40 hours before its test.

The indicated relationship between actual temperatures and orientation angles cannot be stressed, because the so-called surface temperatures were not accurate measurements of the temperatures that really occurred. On the other hand, the relationship shown between changes in temperature and changes in

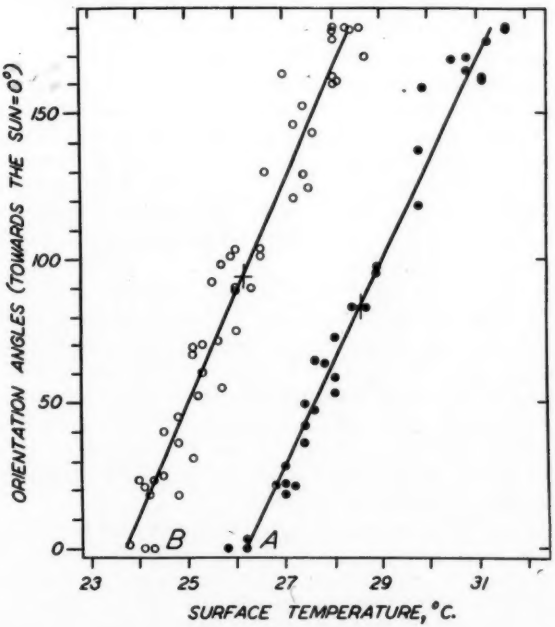

Fig. 5. Changes in orientation with respect to the sun shown by a second-instar *Hyphantria* larva crawling on a sheet of graph paper on the ground. The surface temperatures shown were measured thermoelectrically. Curve A shows the changes in heading in response to temperature changes while the larva was fully fed. Curve B shows the changes after 48 hours starvation. In both instances, the larva was acclimated to 20.5°C. and 50% R. H. for 40 hours before its test.

heading is more trustworthy. To duplicate these results, a clear sky is best, since any fluctuation in turbidity will mask the changes in response to temperature by evoking responses to the changing plane of polarization.

Like *Malacosoma*, mature larvae of *Hyphantria* also engage in some prepupational travel, although distances covered do not appear to be as great. Careful observation of these travelling larvae showed that the short-distance directional changes shown in Fig. 5 occurred, but they tended to be masked by the longer resultant path that had to be observed to obtain an overall heading for such rapidly moving larvae. Measurements of the internal temperatures of these travelling larvae showed that, like *Malacosoma*, they travelled away from the sun when warmed to or above their reaction range (Table I).

Sky conditions were usually unsuitable for polarization tests of larvae younger than the fifth instar, so tests during early instars were inconclusive. When larvae of instars V and VI were tested, however, they responded with 90° shifts in their directions of travel when the polarizer was shifted a corresponding amount (cf. 2, 5, 6, 7). In addition, when heavy smoke passed rapidly overhead, producing rapid changes in the polarization plane, these larvae also exhibited the synchronous turns previously described for larvae of *Neodiprion americanus banksianae* Roh. (7) and more recently discussed in connection with several kinds of insects (6). (This phenomenon is most noticeable when several insects are observed at once. As the smoke drifts overhead in patches, the insects respond simultaneously to changes in the sky by turning right or left together, even when they are separated from one another by intervening walls of cardboard.)

Field Observations

Observations of the reactions of *Hyphantria* larvae to light under natural conditions were made during the course of studies on the effects of weather on the insects. During these studies, it was found that larvae during their feeding stage were much more active at night, or during warm, humid, overcast days than at any other time. General activity, as well as feeding activity, increased markedly during these periods when direct sunlight was not present. Whenever sunlight was present, however, the effects of temperature on the photic orientation of the larvae became important.

Hyphantria larvae of instars I-V do not feed on new leaves in natural environments in Ontario until the leaves are enclosed in a web. During the first three instars, the web of a colony is usually small, and seldom encloses more than a few leaves near the tip of a branch. Consequently, when these young larvae are overheated by direct sunlight, they move directly under the illuminated leaves into a shadowed, cooler recess. Such movements take place in the field when the air inside the web is heated above the reversal range of the instar. Web formation occurs commonly at night or on cloudy, damp days, and is not affected by the light reactions of the larvae.

During the last three instars, particularly during the fourth and fifth, when feeding still takes place within the web, the shelter is much enlarged and contains much more trapped air and foliage in various stages of destruction. At this stage, the web is a very efficient greenhouse during cloudy weather, but temperatures in it rise to extremely high levels when it is exposed to direct sunlight. For example, with an outside air temperature of 33°C., fully exposed hazel leaves were nearly 39°C., but those inside a web rose as high as 46.4°C. (This suggests, incidentally, that the browning of otherwise undamaged leaves commonly observed within older parts of a web may occur partly because the leaves are killed by overheating.) The central, darker portions of the web are even

hotter than the outer layers and, once again, as in *Malacosoma* (3), the much stronger photopositive reaction of overheated older larvae of *Hyphantria* brings them directly and rapidly out of the hot web. Rapid evacuation of the web occurs only when its interior temperatures rise above the reaction range of the instar concerned. Consequently, it is not uncommon to observe fourth-instar larvae leaving the web rapidly while fifth- or early sixth-instar larvae remain within it (Table I).

In these older instars, web formation also occurs most frequently during the night or damp days, but it also occurs during periods of direct sunlight if the larvae are driven from the web. The larvae are not processionary, so they emerge from the web over a broad front, and continue to move over a wide area while they are outside. This milling results in the formation of a loosely woven network that is rapidly filled in because larvae tend to use existing threads for only short distances, and continually strike off from the original thread, putting out new silk as they move. This is the only method of web construction at any time.

When larvae near their prepupal period, they leave the tree. Characteristically, they move to the edge of the web or the end of a twig, hump their backs, and snap quickly into a straight position. This movement throws them outward 6-7 cm. before they begin to fall.

Measurements of the internal temperatures of 50 larvae that were leaving the trees showed that they were all above 30°C. Once on the ground, as noted previously, they travelled in directions ranging from directly towards to directly away from the sun, depending on their internal temperature. If they were cooled below about 30°C., they travelled more or less towards the sun, and 31°C. was the lowest temperature recorded for movement directly away from the sun.

DISCUSSION

In studies of the reactions of insects to light, emphasis is placed sometimes on the behaviour of groups, and sometimes on the behaviour of individuals. Whichever approach is used depends partly on its convenience to the observer but, in any event, results obtained by either method of study generally are discussed in terms of groups. Descriptions of group behaviour, or statistics that help to define behaviour to be expected within a population are always valuable. Occasionally, however, it is worth while to observe the individual for its own sake, and to determine the range of variation of its behaviour patterns. In short, the statistics of the individual sometimes may offer a more rewarding field for investigation than the statistics of the group. This paper is one of the first (cf. 6) in which we have consciously begun to emphasize this approach to studies of changes in orientation. Since the paper as a whole also contains many observations of groups, the treatment of the individual is still subordinated in it, and the success of our newer approach has varied from the wholly qualitative results of Fig. 1 to the quantitative results of Fig. 5. Enough promise is shown, however, to make further quantitative investigations worth while.

In our previous tests of several species of insects, grouped records have shown that starvation often affects the responses of larvae to light, although different species may react in different ways. Indeed, larvae of different instars within the same species frequently show differences in their responses. For example, young larvae of *Choristoneura fumiferana* (Clem.) become more or less indifferent to a point source when starved, whereas older larvae eventually become photonegative (4). On the other hand, larvae of all instars of

Malacosoma spp. simply become more strongly photopositive when starved (3), as do young larvae of *Neodiprion americanus banksianae* Roh. and *N. lecontei* (Fitch) (1). In *N. lecontei*, however, further starvation of older larvae results first in an increase in the number that become indifferent to the light, and finally in a renewed increase in the number that respond photopositively. Therefore, such results have shown that it is necessary to distinguish not only between responses of different species or instars to starvation, but also between the effect of short-term and prolonged starvation. The present series of tests adds another item to this list: differences in the behaviour of an individual between successive trials, whether the larva is fed or starved.

In the younger instars of *Hyphantria*, starvation at first seems to have the same effect as slight warming on the accuracy of orientation of the larvae to a point source, i.e., the initial response of either warm, fed larvae, or cooler, starved larvae is both rapid and accurate. Although the rapidity of the response is preserved during further trials of starved larvae, its directness disappears after one or two trips to the light, and may or may not reappear. The indirect paths of starved larvae certainly cannot be taken as examples of indifference to light, since it has been shown that a moving larva appears to take into account the location of the light source at all times. In the second instar, larvae cannot even be considered to be acting photonegatively in any simple way, since they may suddenly revert to direct trips to the lamp at any instant. The behaviour of third-instar larvae, although still flexible, is more consistent, in that sudden reversions to purely photopositive orientation do not occur, and the "positive" and "negative" legs of the course taken by a larva appear to be confined within a definite zone of intensities.

The flexible behaviour of larvae of the first three instars may have some value in the field, where a search for food often may require short-distance travel inward from the periphery. In any event, it is interesting that a marked division occurs between photic behaviour in the first and last three instars. The behaviour of the last three instars contains no trace of a photonegative response to either directed or diffuse light until just before pupation, when the mature larvae may respond photonegatively to directed light during the period they are apt to crawl under debris to pupate.

Like older larvae of *Choristoneura* (4), starved late-stage larvae of *Hyphantria* can be made to revert to a more direct approach to a point source by ligaturing them. As noted, *Hyphantria* is the only other species we have found to date that will respond in this way.

In addition to the effects noted above, starvation also lowers the temperature at which an individual changes its response to overhead light. Starvation does not appear to complicate further any change in the sign of the reactions to overhead light that may occur at a given temperature: it simply lowers the temperature at which reactions occur. This has also been observed in larvae of *N. americanus banksianae* (1) and in several other kinds of insects (6), but the factors involved are still as obscure as those involved in the changed responses produced by ligatures.

Starvation also lowers the temperature range within which *Hyphantria* larvae change their orientation angle to the sun in response to changing temperature (Fig. 5). At first glance, there seems to be no need to separate this effect of starvation from the one noted above, since they appear to be essentially the same. Evidence is mounting, however, that changes in orientation to the sun in response to changing temperature are changes in orientation to solar *heat*, not light (6). Therefore, it seems preferable to consider that two different reactions

are involved, and that the effect of starvation on both is shown by a reduction of the temperatures at which they occur.

In the past, we have called movements to or away from the sun "photopositive" or "photonegative". With our present information, it is clearly unwise to use these terms to refer to orientations that occur primarily in response to radiant heat. At present there is no such objection to employing these terms to refer to the orientation of insects to a point source of artificial light, or to behaviour in an alternative chamber. Even in the laboratory, however, some redefinition eventually may prove necessary to take into account the more flexible behaviour in response to point-source stimulation described earlier: behaviour that is certainly not evidence of indifference, and that should not yet be classified as a light compass reaction.

It is still not clear what significance, if any, should be read into the reasonably close correspondance between an insect's photic reversal temperature and the temperature at which it begins to travel directly away from solar heat. Probably the only connection is that both temperatures are close to the lethal temperature, so that both are associated with reactions that ordinarily remove the insect from potentially lethal conditions. If this is so, then one could expect to find a similar close correspondence in the maximum temperature to which the insect would move in a temperature gradient, whether or not light is present.

CONCLUSIONS

1. At room temperature, larvae of all instars are initially photopositive to point sources, although young larvae have to be warmed slightly before they will orientate accurately, and older larvae often begin to approach the light indirectly after one or two tests.
2. In younger larvae, starvation produces a change from a photopositive state to a more flexible state in which larvae always move with reference to the location of the light source, but may move at different angles to it, or even directly away from it. Older larvae simply compass more consistently than when fed.
3. Whether fed or starved, all instars react more or less photopositively in a dark-light alternative chamber at room temperature, although the reaction is stronger during the first three instars. At higher temperatures in the chamber, larvae of the first three instars become strongly photonegative, whereas those of the last three simply become more strongly photopositive. Starvation does not influence these changes or modifications in the sign of the reaction, but it does lower the temperature at which they take place, often by 3°C. or more.
4. Outdoors, fed or starved larvae crawling on the ground orientate with respect to the sun. When cool, they travel directly towards it, but turn more and more away from it as they become warmer until, finally, they move directly away from it when overheated. Once again, starvation only lowers the temperature range in which this gradual change takes place.
5. Larvae travelling over the ground at any given temperature maintain their orientation by means of their response to plane polarized light and consequently they will respond to rotation of an overhead polarizer through 90° by changing direction a corresponding amount.

ACKNOWLEDGMENTS

We wish to thank G. W. Green for the loan of some of the apparatus, and for making available results that were unpublished at the time. We also wish to thank Miss P. M. G. West for technical assistance, and J. A. Chapman, Forest Biology Laboratory, Victoria, B.C., for critical reading of the manuscript.

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(Received October 26, 1954)

Euura salicis-nodus (Dalla Torre) (Hymenoptera: Tenthredinidae) and its Hymenopterous Parasites Reared from Spindle-galls of Willow

By W. W. Judd

Department of Zoology, University of Western Ontario
London, Ontario

In a communication previously published (Judd, 1952) the writer reported upon studies of insects reared from Pine Cone Willow galls collected near London, Ontario in 1951. At the time this collection was made numerous galls of another type were noted on the twigs of a growth of willow shrubs adjacent to those from which the Pine Cone galls were taken. These galls were spindle-shaped swellings of the twigs and branches and were from three-quarters to one and one-half inches long and, at their greatest width, two or three times as wide as the twigs (Fig. 1). They were confined to a growth of willow which formed a straggling band along the edge of a field, the individual bushes being shrub-like in stature, three or four feet tall. This willow was identified as the sandbar-willow (*Salix interior* Rowlee) by use of a key to foliage of *Salix* in Fernald (1950). Most of the galls were separate from one another, forming individual swellings along the twigs. Some twigs and branches bore only a few galls but some bore several, there being as many as eight separate galls along one foot of branch. In a few cases two galls were so closely adjacent that they formed a single bilobed swelling of the twig. In the key to insect galls of willow in Felt (1940) they were identified as spindle-galls caused by the sawfly *Euura nodus* Walsh.

A collection of the galls was made on February 15, 1953 and some of these were dissected. Examination of the galls revealed that some were perforated by one or two circular holes 1 mm. in diameter (Fig. 1-A, B, C) while others were unperforated. A gall with a single opening (Fig. 1-A) might have this opening anywhere over the surface but usually it was near one end of the gall.

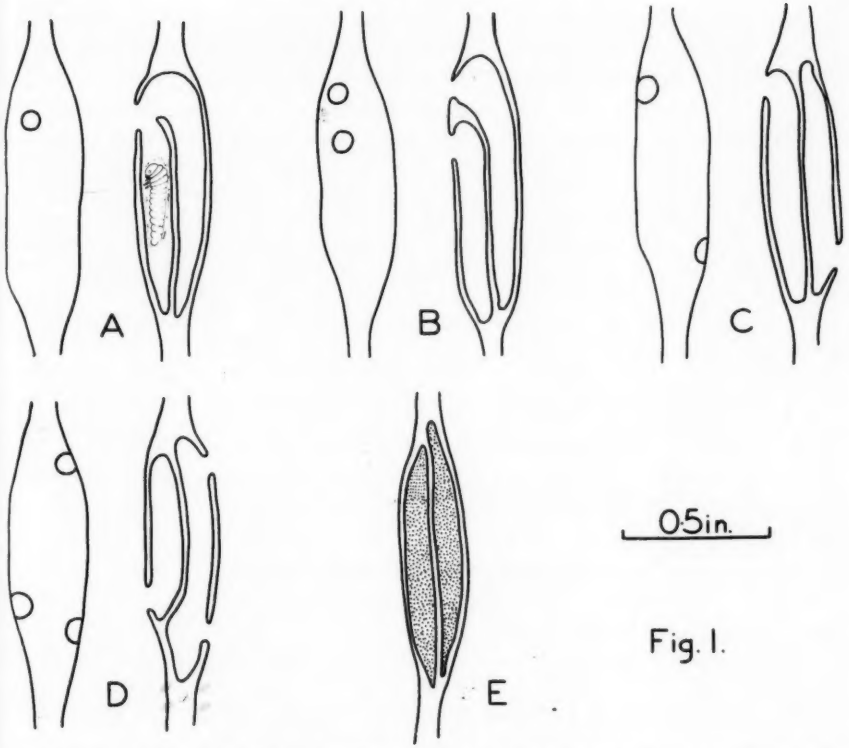

Fig. 1.

A.—External view and longitudinal section of gall with one opening and two chambers; larva of *Euura salicis-nodus* in cocoon in one chamber.
B—External view and longitudinal section of gall with two openings and two chambers.
C.—External view and longitudinal section of gall with two openings and two chambers.
D.—External view and longitudinal section of gall with three openings and two chambers.
E.—Internal view of two-chambered gall with undisturbed wood.

Where two openings were present they might be close together (Fig. 1-B) or widely separated (Fig. 1-C). These openings led into elongated chambers in the gall (Fig. 1-A, B, C) occupied by sawfly larvae, each larva being about one-quarter of an inch long and surrounded by a flimsy cocoon (Fig. 1-A). The remainder of the chamber was filled with brown wood dust and frass surrounding the cocoon. In all cases the larva was placed so that its anterior end was toward an opening of the gall. Most of the galls contained two chambers separated by a tough partition of white wood with a larva in each chamber, the two chambers having a common opening (Fig. 1-A) or two separate openings (Fig. 1-B, C). Some galls contained only a single chamber. Fifty galls were split open in order that the number of larvae in them could be counted and it was found that 20 contained one larva each and 30 contained two larvae. Dissection of an unperforated gall usually disclosed one or two chambers which contained larvae and which extended to the investing layer of the gall but did not perforate it. In this case the larva had evidently extended the chamber to the wall of the gall without piercing it and then retreated into the chamber to spin its cocoon. Some galls, more slender than most, contained the usual two chambers but they were

filled with undisturbed wood (Fig. 1-E) and showed no sign of activity by larvae. In this case the gall had evidently developed following the ovipositing activity of the adult female but the larvae had failed to hatch.

Methods of Rearing

One hundred and fifty intact galls were clipped from the willow twigs on February 15, 1953. Each gall was put in a separate, numbered glass vial of dimensions 60 mm. x 15 mm., plugged with cotton. The vials were kept on a rack and were examined each day for the presence of insects which had emerged from the galls. The insects were killed, pinned and labelled to show the date of their emergence and the number of the gall from which each had emerged. On December 30, 1953 the galls were removed from the vials and dissected and any adult insects found in them were pinned and labelled. Of the 150 galls, 41 produced no insects, 56 yielded one sawfly each, 39 yielded two sawflies each, 2 yielded three sawflies each, 5 yielded one sawfly and one parasitic wasp each and 7 yielded only parasitic wasps. All specimens reared and dissected from the galls are deposited in the collections of the University of Western Ontario except those retained in the Canadian National Collection, Ottawa, as recorded in the following account. Identifications of the specimens were kindly made by taxonomists of the Division of Entomology, Science Service, Department of Agriculture, Ottawa.

Account of Insects Collected

Tenthredinidae

Euura salicis-nodus (Dalla Torre)

Representative specimens of the sawflies reared from the galls were identified by Dr. R. Lambert as *Euura salicis-nodus* (Dalla Torre). Two males and two females are retained in the Canadian National Collection. This species is recorded

TABLE 1

Numbers of *Euura salicis-nodus* that emerged from spindle-galls.

Date	♂	♀	Total	Date	♂	♀	Total	Date	♂	♀	Total
April 1	3	1	4	April 13	4	12	16	April 25	3	1	4
" 2	5	0	5	" 14	6	2	8	" 26	1	1	2
" 3	1	0	1	" 15	4	2	6	" 27	0	1	1
" 4	2	4	6	" 16	1	0	1	" 28	1	0	1
" 5	2	1	3	" 17	4	6	10	" 29	0	2	2
" 6	4	0	4	" 18	1	4	5	" 30	0	1	1
" 7	2	1	3	" 19	1	1	2	May 4	0	1	1
" 8	3	2	5	" 20	1	2	3	" 5	0	1	1
" 9	1	3	4	" 21	2	5	7	" 6	0	1	1
" 10	2	4	6	" 22	0	2	2	" 9	1	0	1
" 11	0	4	4	" 23	0	7	7	" 12	1	1	2
" 12	0	4	4	" 24	0	3	3	TOTAL	56	80	136

by Ross (1951) as being from a stem gall on *Salix interior*. The name *Euura nodus* Walsh, used by Felt (1940), is recorded by Ross as being invalid. During the period April 1 to May 12, 1953 there emerged from the galls 136 sawflies, 56 of these being males and 80 females (Table 1). The maximum number of emergents in one day was 16, on April 13. In addition to the living sawflies reared from the galls 4 male and 5 female specimens were dissected from them on December 30. The galls thus yielded 145 sawflies: 60 (41.3%) males and 85 (58.7%) females. Dissection of the two galls, which had yielded three sawflies each, disclosed that they had two chambers, one with a single opening and the other with two (Fig. 1-D), indicating that of the three larvae developing in each gall one was in one chamber and two in the other. Some of the galls were found to contain shrivelled sawfly larvae that had failed to pupate. Many of the galls among those from which no insects or only one insect emerged contained undisturbed wood in the chambers with no evidence of activity by insects. The distribution of sexes of the sawflies from unparasitized galls and galls containing no dead larvae was as follows: 1 ♂ (21 galls), 1 ♀ (32 galls), 2 ♂ ♂ (9 galls), 2 ♀ ♀ (17 galls), 1 ♂, 1 ♀ (13 galls), 2 ♂ ♂, 1 ♀ (1 gall), 1 ♂, 2 ♀ ♀ (1 gall).

From the data presented above it is concluded that the female *E. salicis-nodus* lays one, two or occasionally three eggs in the twig of *Salix interior* at the site of production of each gall. As the gall develops it becomes spindle-shaped and contains one or two chambers, each with a single larva or possibly two larvae. If an egg fails to hatch the wood in the chamber remains undisturbed. The larva feeds upon the wood and the chamber gradually becomes filled with wood dust and frass. The larva extends the chamber toward one end, either piercing the investing layer of the gall to form an opening or leaving it as a thin membrane over the opening. The larva in its final instar spins a flimsy cocoon surrounded by frass and wood dust and is so situated in the cocoon that its anterior end faces the opening of the chamber. The insect remains in its larval state during the winter, pupating in the spring and emerging later as an adult.

Braconidae

Ichneutes sp.

Two wasps emerged from two galls and were identified as *Ichneutes* sp. by Dr. W. R. M. Mason who retained the two specimens for the Canadian National Collection. A male wasp emerged from one chamber of a gall on April 13, the other chamber yielding a female *E. salicis-nodus* on April 23. A female wasp emerged from one chamber of another gall on April 3 and the other chamber of this gall was found to contain a dead male *E. salicis-nodus* when the gall was dissected on December 30. Muesebeck and Walkley (1951) comment on the subfamily Ichneutinae (including *Ichneutes*) that little is known about the host relations for this group, but that apparently the hosts are sawflies. Thompson (1950) lists several leaf-feeding sawflies as hosts of species of *Ichneutes*.

Ichneumonidae

Hoplocryptus sp.

On April 2 one gall yielded a male *E. salicis-nodus* from one chamber and from the other a male wasp identified by Dr. W. R. M. Mason as *Hoplocryptus* sp. The specimen is deposited in the Canadian National Collection. Known hosts of wasps of this genus, as recorded by Townes and Townes (1951), include a bee of the genus *Ceratina* and some leaf-eating sawflies. Thompson (1950) lists several wasps of the family Vespidae as hosts for various species of *Hoplocryptus*.

Pteromalidae

Habrocytus thyridopterigis Howard

Five dead wasps of this species were retrieved from five galls dissected on December 30, the one male and four female specimens being identified by Dr. O. Peck. Only one of the galls yielded a sawfly, a dead male *E. salicis-nodus*, on December 30. Peck (1951) lists several moths and wasps as hosts of *H. thyridopterigis*.

Eurytomidae

Eurytoma sp.

Five dead wasps, identified by Dr. O. Peck as *Eurytoma* sp. were removed from five galls dissected on December 30. Only one of these galls yielded a sawfly, a male *E. salicis-nodus*, on April 4. One of the wasps was found in company with a female *Habrocytus thyridopterigis* in one chamber of a gall, the other chamber containing a shrivelled sawfly larva. Peck (1951) lists many insect galls on plants as hosts for various species of *Eurytoma*, including several willow galls caused by sawflies of the genus *Euura*.

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(Received October 26, 1954)

Notes on a Polyhedral Disease of Black-Headed Budworm[1]

By KENNETH GRAHAM
Department of Zoology, University of British Columbia
Vancouver, Canada

A polyhedral disease was discovered to be one of the natural agents attacking the black-headed budworm, *Acleris variana* (Fern.) in the coastal region of British Columbia during the outbreak of this insect, 1940-45. This disease became the most important single factor contributing to the decline of the outbreak (Prebble and Graham 1). The present report includes observations on some of the symptoms and microscopic characteristics of the disease.

Typical polyhedral disease was identified in larvae in their last four instars, but most often in the last (fifth), and in pupae. Males and females of these stages were apparently equally affected. Search for pathological symptoms in the moths yielded no signs, despite other evidence that they could convey the disease to their progeny through the eggs.

The polyhedral disease in *Acleris* larvae was manifested externally by sluggishness, pale mottling and opacity of the hypodermis, the body colour becoming

[1]Contribution No. 163, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

ash-grey. The body became swollen, the tissues liquefying without odour, and the skin so fragile that the insect could not be picked up intact. In pupae, also, extreme liquefaction of the tissues and fragility of the skin occurred, and the abdominal segments were generally retracted. The frank form of the disease occurred mostly during August, i.e. affecting the last-instar larvae and pupae.

Microscopically, the disease was characterized by the hypertrophy of the nuclei as the numerous polyhedral inclusions (Fig. 1) developed to replace the

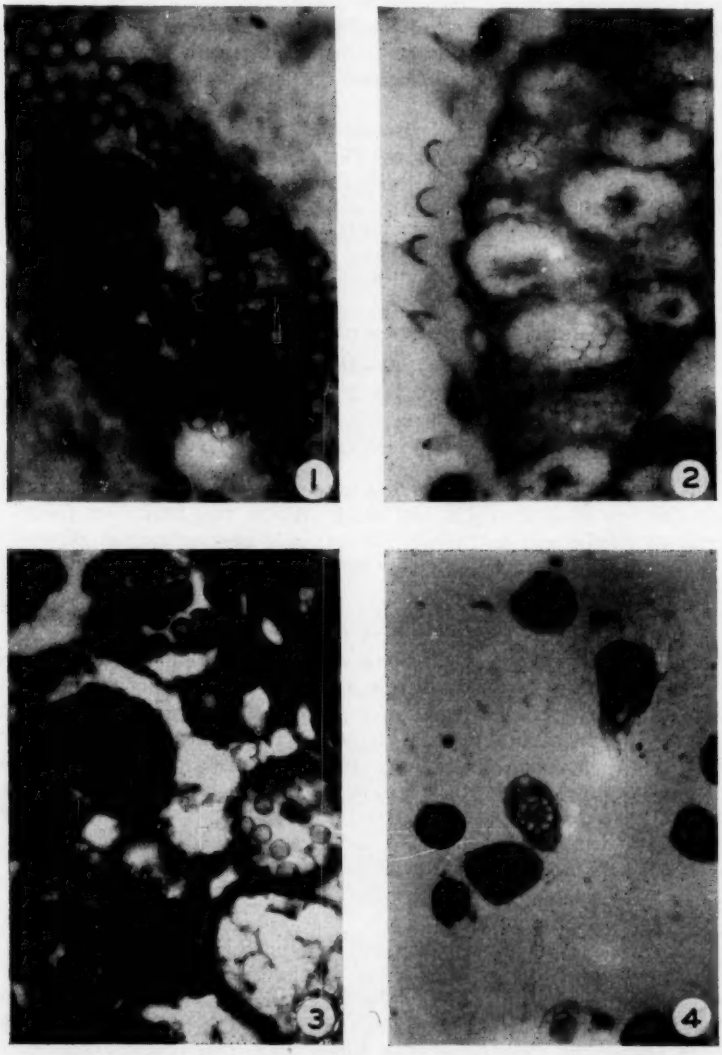

Fig. 1. Polyhedral bodies in advanced stage of disease. x1600.
Fig. 2. Section through diseased hypodermis. Note great hypertrophy of nuclei filled with polyhedral bodies. x800.
Fig. 3. Advanced stage of disease in nuclei of fat-body cells. x1500.
Fig. 4. Intranuclear polyhedral bodies symptomatic of disease in blood cell. x800.

nuclear mass and distend the nuclear membrane. The tissues affected included especially the hypodermis (Fig. 2) and fat-body (Fig. 3), but occasionally the blood cells (Fig. 4), and very rarely the muscle cells, tracheal matrix, and pericardium were involved. Nerve cells, silk gland and duct, digestive epithelium, foregut, hind gut, rectal and Malpighian tubule cells revealed no symptoms.

This polyhedral disease was first observed in 1941 in pupae from the Cascade Creek infestation in the lower Fraser Valley where it reduced the *Acleris* infestation to a very low level. The same disease became manifest in 1942 in a rising population of *Acleris* in the Cottonwood Creek infestation on Vancouver Island, where it controlled the infestation within the subsequent two years. Similarly, infestations in the Great Central Lake and Quatsino regions of Vancouver Island were controlled by the disease.

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(Received July 12, 1954)

A New Genus and New Species of Deltocephaline Leafhoppers from Canada and Alaska (Homoptera: Cicadellidae)[1]

By Bryan P. Beirne[2]
Systematic Entomology Unit, Entomology Division
Ottawa, Canada

The following are descriptions of a new genus and two new species of leafhoppers allied to *Streptanus* Rib. and *Macustus* Rib. that have been found in the Subarctic of Alaska and northwest Canada, of a new species of *Hardya* Edw. from the same region, and of the two new species of *Hebecephalus* DeL. from the mountains of Western Canada.

***Coulinus* n. gen.**

Robust, moderate-sized insects, about 4.0 to 5.0 mm. long. Head but slightly wider than pronotum; anterior margin rounded to the front; clypellus broad and weakly convex; vertex broad, convex, median length about 1½ times length next the eye. Pronotum broad, with lateral margins short, weakly carinate. Forewing with appendix small, inner anteapical cell open or closed basally. Abdomen exceeding forewing in length in female. Male genitalia with aedoeagus symmetrical, flattened, strongly recurved, with a pair of long processes arising from the sides of the shaft before the middle and curved dorsally, and with the gonopore subterminal on the posterior surface of shaft; spinelike setae on male plates uniseriate; tenth segment not sclerotized dorsally.

Genotype: *Coulinus uladus* n. sp.

This genus is characterized primarily by the form of the aedoeagus. It is allied to *Streptanus* Rib. but differs in the unsclerotized dorsal region of the male tenth segment, as well as in aedoeagal characters, and to *Macustus* Rib. but differs in aedoeagal and other characters. It is evidently the genus described by Oman (1949) as *Doliotettix* (*nec* Rib.), but differs from that genus, as described by Ribaut (1942), in aedoeagal and other characters. A species of *Doliotettix* Rib. has been found recently in Alaska and is recorded elsewhere (Beirne, in press).

[1]Contribution No. 3224. Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.
[2]Agricultural Research Officer.

***Coulinus uladus* n. sp.**

Fig. 1

Length 4.5-5.25 mm. A broad, robust insect, structurally as described above. Light brownish-ochreous with fuscous and black markings. Face with sutures black; clypellus with black median line; clypeus with two black lines and black lateral arcs; vertex with black transverse band, broadened medially, a pair of black triangles near apex, each sometimes connected by a black line to a black spot surrounding each ocellus, and a black spot near each posterior corner. Pronotum with irregular black spots near anterior margin and with disc usually irregularly suffused fuscous or blackish; scutellum with a pair of black spots on disc and a black median line above transverse impression; thorax largely black beneath; legs irregularly spotted with black. Abdomen largely black above, with posterior and lateral margins of segments pale, largely yellowish beneath, with posterior margins of segments black. Forewing ochreous-greyish, cells mottled and suffused fuscous, especially bordering the veins, the fuscous markings variable in intensity and most pronounced in the claval cells near the commissure and at th ends of the discal, subapical, and apical cells. Internal male genitalia as in the generic description. Female seventh sternum with posterolateral corners shallowly emarginate and with posterior margin roundedly emarginate at either side of a rounded median projection; broadly black along posterior margin, except at sides, and at basal corners.

The genitalic characters are distinctive. On external characters the unbroken median transverse band of the vertex distinguishes the species from related species that it resembles superficially, other than the following species and *Streptanus marginatus* (Kirsch.), which, however, are smaller insects that have the forewings much less heavily dark-marked.

Holotype, ♂:—on tundra, Naknek River, Alaska, July 7, 1952 (W. R. M. Mason). No. 6151 in the Canadian National Collection, Ottawa.

Allotype, ♀:—Mile 149, Richardson Highway, Alaska, July 4, 1951 (W. R. M. Mason).

Paratypes:—2 ♂, on tundra, Naknek, Alaska, July 17, 1952 (W. R. M. Mason); 2 ♂, 4 ♀, King Salmon, Naknek River, Alaska, July 8-19, 1952 (W. R. M. Mason); 2 ♂, same data as allotype; 1 ♂, Mile 142, Richardson Highway, Alaska, July 4, 1951 (W. R. M. Mason); 1 ♂, 1 ♀, Great Whale River, Quebec, July 18 and 2, 1949 (J. R. Vockeroth).

***Coulinus usnus* n. sp.**

Fig. 2

Length 3.5-4.0 mm.; a rather robust insect, structurally as in the generic description. Light brownish-ochreous with brownish, dark-fuscous, or blackish markings. Face with sutures blackish; clypeus with longitudinal bands and lateral arcs fuscous or black and face often largely black; vertex with a median brown, fuscous, or black transverse band that is broadened at middle, a pair of dark lines at anterior margin, and sometimes a pair of dark triangles near apex. Pronotum with a pair of dark median spots near anterior margin and sometimes other, irregular dark spots near anterior margin and on disc; thorax largely black beneath; legs variably marked with black or fuscous; scutellum usually with a pair of dark spots on disc and a pair of dark spots, or a dark area, below transverse impression. Forewing brownish-ochreous, usually mottled fuscous along the commissure, and the apical cells suffused fuscous or brownish near the margin of the wing; sometimes all or most of the veins outlined with brownish or fuscous spots. Abdomen largely black, with the posterior margins of the segments

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usually pale. Internal male genitalia as in the generic description. Female seventh sternum with posterior margin sloping from each posterolateral corner to a median incised projection, and with a broad black band bordering posterior margin from middle to near posterolateral corners.

The genitalic characters are distinctive. This is a smaller and less distinctly dark-marked insect than *Coulinus uladus* n. sp. On a basis of external characters and size it resembles *Streptanus marginatus* (Kirsch.), which also has an unbroken median transverse band on the vertex, but can be distinguished easily by genitalic characters.

Holotype, ♂:—Muskox Lake, lat. 64.45 N., long. 108.10 W., Northwest Territories, July 17-21, 1953 (J. G. Chillcott). No. 6152 in the Canadian National Collection, Ottawa.

Allotype, ♀:—same locality and collector as holotype, August 2-6, 1953.

Paratypes:—12 ♂, 7 ♀, same locality and collector as holotype, July 4 to August 6, 1953; 1 ♂, Aklavik, Northwest Territories, Yukon, June 20, 1953 (C. D. Bird); 3 ♂, 2 ♀, altitude 3800 ft., Mile 109, Steese Highway, Alaska, June 21, 1951 (Mason and McGillis); 9 ♂, 2 ♀, Salmita Mines, lat. 64.05 N., long. 111.15 W., Northwest Territories, June 17-22, 1953 (J. G. Chillcott).

Key to Species of *Coulinus*

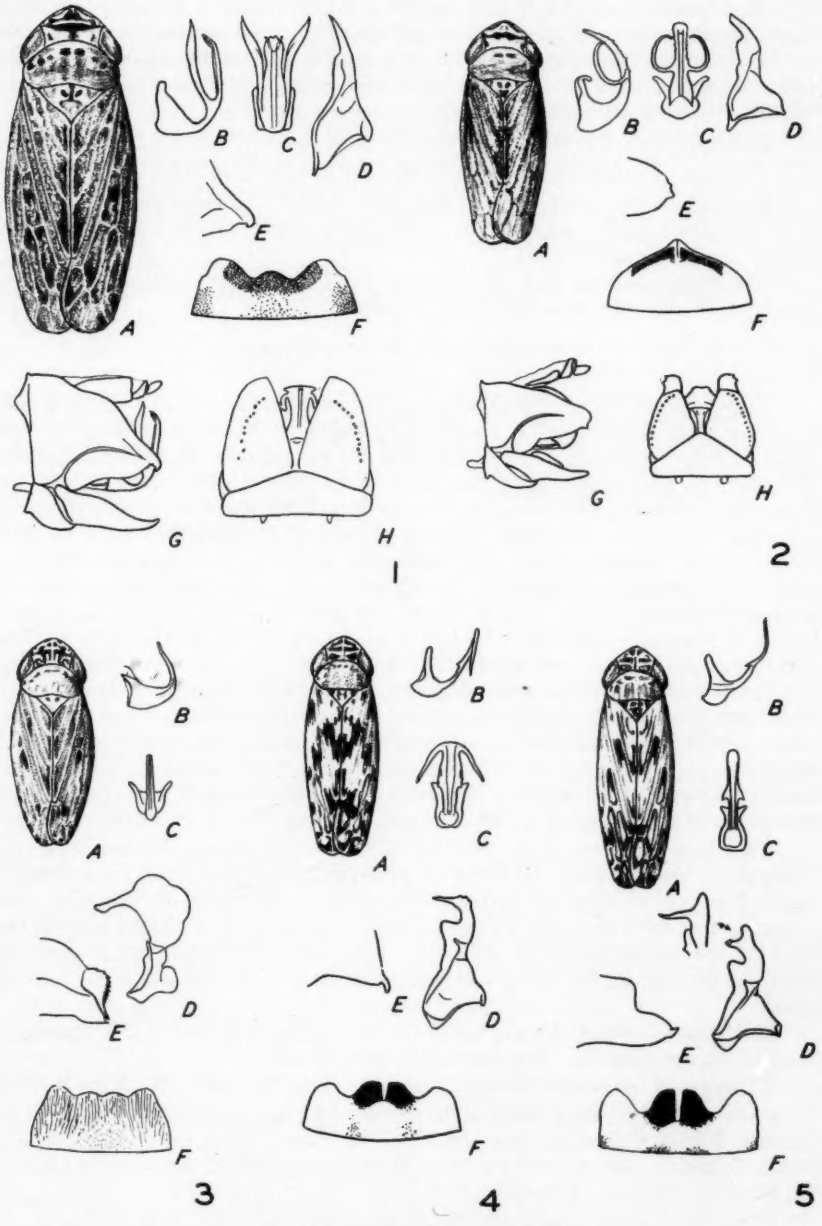
Larger species, 4.5-5.25 mm. long; forewing with cells distinctly margined or suffused fuscous; processes of aedoeagus flattened, less strongly curved, extending dorsally to beyond apex of shaft; shaft with a subterminal pair of spine-like processes on ventral surface; male pygofer with a stout hook at apex; female seventh sternum with posterior margin emarginate at either side of a rounded median projection ..... *uladus* n. sp.

Smaller species, 3.5-4.0 mm. long; forewing usually with weak and indefinite dark markings, not as above; processes of aedoeagus not flattened, strongly curved dorsally and posteriorly; apical region of shaft without processes; apical region of male pygofer rounded, with two, short projections; female seventh sternum with posterior margin evenly sloping to a median, incised projection ..... *usnus* n. sp.

***Hardya youngi* n. sp.**

Fig. 3

Length 3.0-3.5 mm. Head ochreous; clypellus with a black median line; a black area surrounding each antennal pit; clypeus with two longitudinal fuscous bands, usually confluent anteriorly, and fuscous lateral arcs; vertex brownish-ochreous medially and laterally, with brownish or fuscous markings as follows: a median transverse band, interrupted at middle, from the lower margin of which two pairs of lines extend to near the posterior margin of the vertex, where the outermost of each pair meets a darkened ring; and a pair of triangles near the apex of the vertex, each often confluent with a short streak extending from the upper margin of the median band. Pronotum ochreous, with brown or reddish-brown markings near anterior margin, and often weakly tinged fuscous on disc; scutellum with a median pair of dark-brown or fuscous spots and with a pair of whitish-ochreous longitudinal bands; ventral surface of thorax largely black; legs yellow, femora with variable dark lines and tarsi usually darkened. Forewing smoky with the veins ochreous, and usually with fuscous suffusions in the claval cells along the commissure, at the apices of the apical cells, and at the bases and apices of the subapical cells. Abdomen usually black except at the sides. Internal male genitalia with apical half of style broad, irregularly rounded, with a lateral arm; apical region of pygofer strongly sclerotized, its upper and caudal margins with spines, and with a long downwardly directed spine below. Female seventh sternum with numerous, irregular, longitudinal striae; posterior margin with lateral corners produced and with a low, rounded projection at either side of a median notch.



Figs. 1-5. New species of deltocephaline leafhoppers: 1, *Coulinus uladus* n. sp.; 2, *C. usmus* n. sp.; 3, *Hardya youngi* n. sp.; 4, *Hebecephalus mornus* n. sp.; 5, *H. creimus* n. sp.

A, whole insect; B, aedoeagus, lateral view; C, aedoeagus, posterior view; D, style; E, apical region of male pygofer; F, female seventh sternum; G, male genitalia, lateral view; H, male genitalia, ventral view.

This species resembles *H. dentata* (O. & B.) on a basis of external characters, but is slightly larger and more robust and usually has the median transverse band of the vertex reaching the eyes. The two species are readily separable on genitalic characters, notably the male style and pygofer and the female seventh sternum. The distributions probably do not overlap.

Holotype, ♂:—Point Barrow, Alaska, June 29, 1953 (P. D. Hurd).

Allotype, ♀:—same locality and collector as holotype, June 26, 1953.

Paratypes:—3 ♀, same data as holotype; 3 ♂, 11 ♀, same data as allotype; 1 ♂, 1 ♀, same locality and collector as holotype, June 17, 1953; 1 ♀, do., June 14, 1953; 1 ♀, do., June 28, 1953.

Holotype, allotype, and paratypes in the United States National Museum, paratypes in the Canadian National Collection, Ottawa.

Hebecephalus mornus n. sp.

Fig. 4

Length 3.0-3.5 mm. Head whitish-ochreous; facial sutures broadly black; clypellus black below and on mid-line; clypeus with black lateral arcs that are often confluent but with a rounded, yellowish, median area below middle; vertex with three pairs of brown spots, the two anterior pairs usually confluent laterally. Pronotum ochreous, with irregular brown spots near anterior margin and with brownish irrorations, sometimes forming indefinite, longitudinal bands, on disc; thorax largely black beneath; femora banded dark brown; scutellum ochreous, with basal triangles, a median pair of spots, and a pair of spots below the transverse impression brown or dark brown. Forewing greyish-white, the cells irregularly bordered internally with dark brown and often suffused dark brown at their ends, particularly in the median and apical parts of the wing. Aedoeagus rather broad, with apex rounded, apical processes directed downward in ventral view, shaft narrowed below a pair of short, pointed dorsolateral projections just below middle, and a pair of minute projections just beyond middle; style with lateral apical processes almost straight; male pygofer with a short, stout, curved hook at posteroventral corner. Female seventh sternum with posterior margin emarginate at either side of a pair of broad, black, median projections.

This is a rather strongly marked species. The aedoeagus and style are distinctive. Other known species of the genus that have the apex of the aedoeagus rounded in ventral view lack pointed dorsolateral projections on the shaft, and in species that have such projections the apex is pointed or produced beyond the bases of the apical processes, or both. No reliable characters, other than the distributions, that distinguish the female from that of *occidentalis* B. & T. were found.

Holotype, ♂:—Soda Creek, Brtish Columbia, June 13, 1950 (G. J. Spencer). No. 6153 in the Canadian National Collection, Ottawa.

Allotype, ♀:—Quesnel, British Columbia, June 30, 1949 (R. Stace-Smith).

Paratypes:—2 ♂, same data as holotype; 1 ♂, same data as allotype; 1 ♂, Quesnel, British Columbia, June 26, 1949 (R. Stace-Smith); 1 ♀, Soda Creek, British Columbia, July 8, 1949 (R. Stace-Smith); 1 ♀, Soda Creek, British Columbia, June 19, 1950 (G. J. Spencer).

Hebecephalus creinus n. sp.

Fig. 5

Length 3.5-4.0 mm. Head pale ochreous; facial sutures black; clypellus with a broad, black, median band, except at base; clypeus with black, confluent, lateral arcs, apical region largely pale; vertex with three pairs of brown or dark-brown

spots. Pronotum with three pairs of irregular, brown spots near anterior margin, and with indefinite, brownish, longitudinal bands; scutellum with basal triangles, a median pair of spots, and a pair of spots below the transverse impression brown or dark brown; thorax largely black underneath; femora banded brown and tibiae with brown spots. Forewings greyish-white with the cells margined internally with dark brown. Abdomen black, pale at sides. Aedoeagus slender, weakly sinuate in lateral view, in dorsal view with a pair of short, broad, lateral processes before middle and with apex rounded; style with apex produced and rounded, and with the lateral apical process long and strongly curved inward; male pygofer with dorsal margin broadly emarginate before apex, at which there is a short, posteriorly directed, pointed process. Female seventh sternum with posterior margin deeply emarginate at either side of a median pair of large, broad, rounded, black projections.

This is a rather large species with the forewing less distinctly marked than in *mornus*. The male pygofer, aedoeagus, and style are distinctive. The relatively large median projections of the female seventh sternum, the deep incision between them, and the deep emargination outside each are distinctive. The species is perhaps most closely related to *callidus* (Ball), which it resembles in form of the aedoeagus but which differs in other characters of the male genitalia.

Holotype, ♂:—Nordegg, Alberta, July 31, 1921 (J. McDunnough). No. 6154 in the Canadian National Collection, Ottawa.

Allotype, ♀:—same data as holotype.

Paratypes:—2 ♀, same data as holotype; 1 ♀, same locality and collector as holotype, July 26, 1921; 1 ♀, do., August 6, 1921.

Acknowledgments

The author wishes to express his sincere thanks to Dr. D. A. Young, Jr., Entomological Research Branch, United States Department of Agriculture, for supplying the specimens of the new species of *Hardya* for description, and for other assistance; and to Dr. F. Ossiannilsson, Lund, Sweden, for the loan of specimens of European species closely related to some of those described above.

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(Received July 19, 1954)

Determination of the Constants Employed in Calculating the Surface Area of the Grasshopper *Melanoplus bivittatus* (Say) (Orthoptera: Acrididae)[1]

By W. CHEFURKA[2] AND J. H. PEPPER[3]

Introduction

In a study of the effects of temperature on the evaporation from the cuticle of the grasshopper, *Melanoplus bivittatus* (3), it was essential to know the surface area of the insect. Because no such information is available for this species and because the surface area of insects rarely varies as the two-thirds power of the weight, an attempt was made to determine the constants of the Meeh formula, $S=kW^n$ (5) which would best correlate the surface area and the weight.

Methods and Materials

The grasshoppers used in this study were reared from field-collected eggs. The eggs, after being in contact with moisture for 24 hours at room temperature in the laboratory, were placed in a rearing chamber in a constant temperature cabinet held at 27.0 ± 0.3°C., and approximately 100% humidity. The rearing chamber, 12 inches x 6 inches x 4 inches, was made of plaster of Paris, the open top being covered by a black plate of glass. Two glass tubes, approximately 6 inches long and 2 inches in diameter and closed at one end, were fitted into two holes in one side of the chamber. As the grasshoppers hatched, they congregated in these glass tubes.

Following hatching, they were transferred from the above small tubes into glass tubes approximately 18 inches long and 4 inches in diameter and closed at both ends by a screen cap. After the grasshoppers reached the fourth instar, they were transferred to small screen cages. All the grasshoppers were then reared at 29.5 ± 0.3°C. and 35% relative humidity. Under these conditions of temperature and humidity, a low mortality and a rapid development were obtained. The animals were fed once a day on a mixed diet of fresh dandelion (*Taraxacum officinale*) and Kentucky blue grass (*Poa pratensis*) when available, and lettuce (*Lactaca sativa capitata*) when the foods were unavailable.

The method used to determine the surface area was similar to that described by Simanton (7). Immediately after weighing, the insects were killed and the head, legs, and antennae were removed for measurement. The abdomen and thorax were cut open, the viscera removed, and the fat body cleaned away by swabbing with cotton and the cuticle was then cut into small pieces. The various body parts were placed between two glass slides which were inserted into a microprojector and the image, which was reflected on a sheet of paper, was traced out.

The areas of all the traced images were determined by means of a planimeter. Because only one side of the legs, antennae, and wing pads was measured, the calculated area of these parts was doubled. The sum of the areas of all the parts gave the total area of the grasshopper. In this manner, the surface area of 66 grasshoppers in all stages of development was measured.

The data were then fitted into Meeh's formula, $S = k W^n$,

S = surface area in square millimeters
k = constant for the species
W = weight in milligrams
n = power of the weight

[1]Contribution No. 3244, Division of Entomology, Science Service, Canada Department of Agriculture, Ottawa, Canada, and Montana State College Agricultural Experiment Station, Bozeman, Montana, U.S.A., Project No. MS 799, Paper No. 304, Journal Series.

[2]Agricultural Research Officer, Field Crop Insect Laboratory, Lethbridge, Alberta. Present address: Science Service Laboratory, London, Ontario.

[3]Department of Zoology and Entomology, Montana State College, Bozeman, Montana, U.S.A.

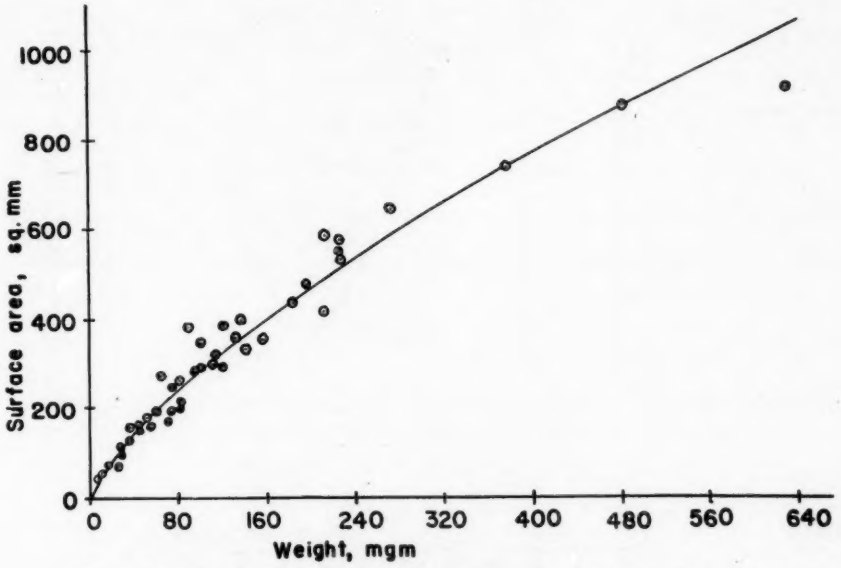

Fig. 1. Relationship between the surface area and weight of grasshoppers.
O Observed area — Calculated area

Results

The use of the Meeh formula depends upon a knowledge of the values of the constants k and n. The average of k was calculated using the experimentally determined surface areas and weights and arbitrarily chosen values of n which ranged from 0.4 to 0.9. The standard deviation of the average value of k was then obtained for each arbitrary value of n that was employed. This deviation was then expressed as a percentage of the average value of k; i.e., $\frac{\sigma}{k} \times 100$ for each value of n. The per cent standard deviation was then plotted against the exponent value, n. The value of n which best fitted the data was that for which the per cent standard deviation of k was minimum. The corresponding value of k was then the most appropriate.

The weights with their corresponding surface areas are represented by the points in Figure 1. From Figure 2 it will be seen that the smallest per cent standard deviation of the average value of k occurred for the exponent value of 0.72, the corresponding value of k being 10.27. The formula used for calculation of the surface area therefore was $S = 10.27\ W^{.72}$ where W = weight in milligrams and S = surface area in square millimeters. The solid line in Figure 1 represents this formula and it is seen to conform with the experimentally determined values represented by the points.

Discussion

The results presented here indicate that the surface area of *M. bivittatus* does not vary with the two-thirds power of the weight. This is in contrast to *Melanoplus femur-rubrum*, *Melanoplus differentialis* and *Locusta* whose surface areas appear to vary with the two-thirds power of the weight (1, 2). Other insects whose areas do not obey the two-thirds power rule are the German cockroach, n = 0.63 and the bean aphid n = 0.60 (7) and *Blatta*, n = 0.75–0.80 (4).

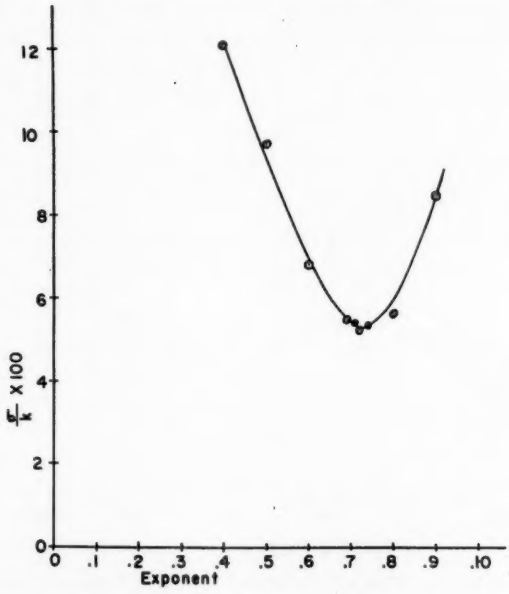

Fig. 2. Determination of the most appropriate value of n.

It is known that the exponent n may vary considerably among individuals of the same species when they are reared under different conditions. Teissier (8) found that the value of n for *Tenebrio* is dependent upon the diet of this insect and particularly on whether or not the animal has been starved. Under such conditions the exponent value varied from 1.0–0.7. This might explain in part the variation of 0.3-1.0 in the exponent value obtained by Michal (6) on *Tenebrio*. This situation probably will necessitate the incorporation of a "nutritional factor" into the Meeh formula where different rearing diets are employed.

Even a greater variation is found among the values of k for different species. For the German cockroach $k = 12.17$, while for the aphid it is 3.28 (7). Wigglesworth (9) employed a value of 8.0 for the larvae of several species of insects. The present studies indicate a value of 10.27 for the two-striped grasshopper.

Summary and Conclusions

Meeh's formula relating surface area to weight was fitted to the data obtained by measuring the surface areas of the cuticles of weighed specimens of the grasshopper *M. bivittatus*. The relationship between surface area and weight was found to be best expressed by the formula.

$$S = 10.27\ W^{.72}.$$

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Influence of Temperature on Embryonic Development of the Pale Western Cutworm, *Agrotis orthogonia* Morr. (Lepidoptera: Phalaenidae)[1]

By I. S. LINDSAY[2]

Field Crop Insect Section, Science Service Laboratory
Lethbridge, Alberta

This is a report on the influence of temperature on embryonic development of the pale western cutworm, *Agrotis orthogonia* Morr. Gross observations on embryonic progress were recorded.

As cultures of this species are continuously needed for studies at the Lethbridge laboratory, information on conditions for adequate egg storage was required. The record of embryonic development was used to determine the most satisfactory stage at which eggs could be stored for future use.

The eggs of the pale western cutworm are laid in loose soil during the last two weeks of August and in early September. There is apparently no diapause and embryonic development may proceed immediately. Temperature fluctuations in the field in the autumn are such that the eggs may be subjected to below-freezing periods. Experiments centred on the effects of the extreme temperatures to which eggs may be exposed.

Materials and Methods

Freshly deposited eggs were sifted out of the soil from oviposition jars. These eggs were then incubated at various temperatures in small culture dishes. A layer of blotting paper in each dish was kept moist to prevent desiccation of the eggs.

The eggs were placed in controlled temperature rooms, which varied within $\pm$ 0.25°C. Daily observations of development were made by dissecting the embryo from the egg and examining it microscopically on a glass slide. Magnifications of 6X to 40X were used in these examinations.

Eggs from both field-reared and laboratory-reared moths were used in the experiments.

1Contribution No. 3250, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada; based on a thesis submitted to the Department of Entomology, University of Alberta, Edmonton, in partial fulfilment of the requirements for the M.Sc. degree, 1952.

2Agricultural Research Officer; now of the Defence Research Board, Suffield Experimental Station, Ralston, Alberta.

Key to Embryonic Development of the Pale Western Cutworm at 30°C.

As this key is intended for a convenient, practical reference to the development of the embryo at 30°C., the time factor is given in days.

Days After Oviposition	Designation on Graph	Stage of Development
0	–	Grey, homogeneous yolk present.
1	A	Two or three small, translucent droplets in yolk.
2	B	Many small, translucent droplets in yolk. A cellular, colourless membrane, the serosa, completed beneath and next to the chorion.
3	C	One translucent mass, the embryo, larger than other droplets in the yolk.
4	D	Embryo a segmented, translucent, elongated mass. Ocelli two small, tan spots. Outlines of mandibles and appendages visible.
5	E	Ocelli reddish-brown and visible through the clean chorion of whole egg. Tan-coloured mass of nerve tissue present in prothorax.
6	F	Tan nerve tissue in each thoracic segment and in the seven anterior abdominal segments. Biting edges of mandibles pigmented. Setae and spiracles visible. Head capsule and cervical shield light grey.
7	G	Mandibles darkly pigmented. Other mouth parts darkening. Head capsule and cervical shield medium grey. Egg still containing yolk.
8	H	Yolk ingested by embryo. Head capsule and cervical shield dark grey.
9	I	Head capsule and cervical shield black and shiny. Abdomen white. Chorion of a whole egg sometimes showing blue tinge.
10	J	Chorion of a whole egg blue-purple with a pearly lustre. Abdomen light tan.
11	K	Abdomen dark tan. Larvae beginning to hatch.

Rates of development varied slightly among embryos. The acquisition of the pearly blue colour by the developing egg coincided closely with the ingestion of the yolk by the embryo. This colour may be the result of air replacing the fluids between the chorion and the embryo.

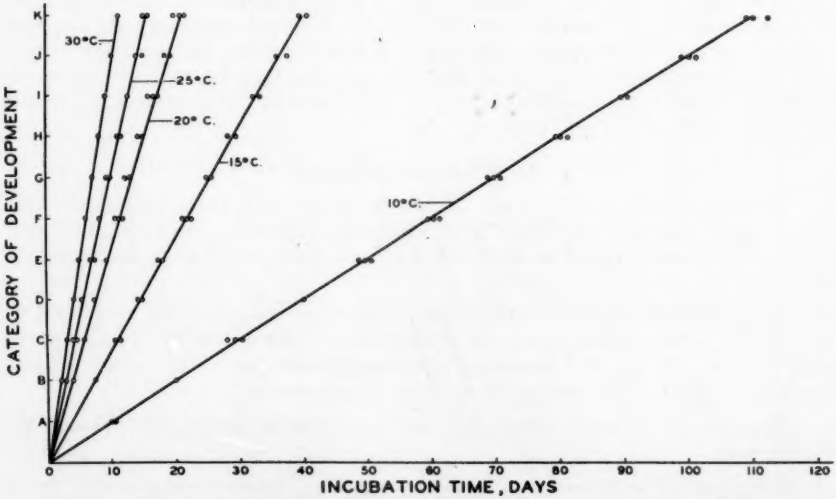

Fig. 1. Embryonic development of *A. orthogonia*, using the categories of development as in the key, at various temperatures.

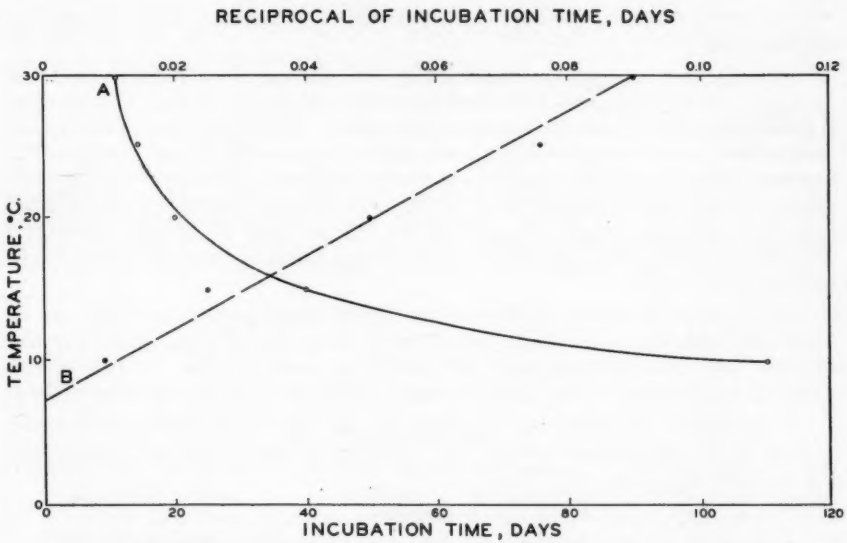

Fig. 2. Effects of temperature on the developmental period of eggs of *A. orthogonia* (data as in Fig. 1). Curve A shows temperature against incubation time. Curve B shows temperature against the reciprocal of incubation time.

Eggs from field-reared and laboratory-reared adults developed at the same rate.

Influence of Temperature

The rates of development of eggs at temperatures of 10°C., 15°C., 20°C., and 25°C. were determined; in all tests, control groups of eggs were incubated at 30°C. (Fig. 1).

Fig. 2 shows that plotting the temperature against the incubation time in days gives a negative correlation. Plotting the temperature against the reciprocal of the incubation time results in a straight line. Although extrapolation of this time-temperature curve indicated the threshold temperature of development to be approximately 8°C., it is probably somewhat less as shown by the recent work of Spring Lin *et al.* (in press). Investigation showed that eggs completed development at 10°C. but not at 5°C.

Eggs incubated at 35°C. appeared to develop normally until stage G. None of these eggs showed the yolk to have been ingested by the embryo. The head capsules were wrinkled and all embryos were eventually killed in this environment. However, the matter surrounding the embryo was always fluid when the embryo died.

Freshly deposited groups of eggs were exposed to 35°C. for 3½, 7, or 14 days and then transferred to 30°C. to complete their incubation period. Embryos of the 3½-day group completed development and normal hatching occurred. No natural hatching took place in either the 7- or the the 14-day group.

When embryonically undeveloped eggs were incubated at 5°C., only slight development occurred regardless of the length of the exposure period. After 90 days the serosal membrane was complete and several translucent droplets were present in the yolk. No further visible development took place at this

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temperature. After a 210-day period all the egg contents showed signs of deterioration.

Groups of fresh eggs were exposed to 5°C. for one, two, four, eight, 16 or 32 days. At the completion of these exposure periods the various groups were transferred to 30°C. and development was noted. A two-day exposure to 5°C. had no effect on subsequent embryonic development at 30°C. When the 5°C. exposure period was four or eight days, the normal hatch decreased from approximately 85 per cent to slightly over 60 per cent and the number of deteriorated eggs increased accordingly. Approximately 10 per cent of the eggs developed normally after a 16-day exposure, whereas all eggs failed to hatch after the 32-day period at 5°C.

Many eggs deteriorated after the 16-day exposure period; in a number of them the embryos were distorted. Mouth parts, larval eyes, head capsule, thoracic legs, and abdomen were all subject to malformation. A few of the distorted embryos were alive after dissection from the eggs but most were dead.

Additional experiments showed that if fresh eggs were incubated for five days at 30°C., then transferred to 5°C., many embryos completed development and hatched normally.

Discussion

Eggs of *A. orthogonia* mature embryonically in 480 hours at 20°C. (68°F.). By comparison Rempel (1951) found that at room temperature (68°-72°F.) the egg of another phalaenid, *Mamestra configurata* Wlk., required 130 hours of incubation.

The experiments conducted at 35°C. showed that freshly deposited eggs will withstand a 3½-day exposure at this temperature but not a seven-day period. This suggests that an essential physiological process is impeded sometime between 3½ and seven days. However, this interference did not affect the progress of the embryo morphologically.

Similarly, the fact that fresh eggs will only develop to approximately stage B of the key at 5°C. unless the eggs are first incubated for a period at a favourable temperature, e.g., five days at 30°C., indicates hindrance of an early physiological system in the embryo. Normally, when this process is functioning or has functioned, embryonic development proceeds to completion at 5°C.

This partial or entire inhibition of an essential enzyme or hormone system at 5°C. may also be responsible for the irregular cell differentiation in the early embryo, which resulted in its distortion and malformation. Church and Salt (1952) found abnormal development in embryos of *Melanoplus bivittatus* (Say) after exposures to temperatures below the theoretical threshold of development. They postulated that the many coincident physiological reactions in the embryo have "individual and somewhat different temperature-activity relations". The present work with the pale western cutworm supports this theory.

Summary

Eggs of *Agrotis orthogonia* Morr. mature embryonically and hatch at constant temperatures of 10°C., 15°C., 20°C., 25°C., and 30°C. A morphological key to embryonic development at 30°C. is given.

At 5°C. eggs failed to complete development normally unless partially developed previously at a favourable temperature. Exposure of fresh eggs to 5°C. for more than a two-day period caused a rapid decline in the number reaching maturity.

No undeveloped eggs withstood a period of seven days at 35°C. but a 3½-day exposure at this temperature, prior to being transferred to a beneficial environment, did not affect normal embryonic development.

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(Received October 26, 1954)

Book Review

TERRICOLE DIPTERENLARVEN, by Adolf Brauns. Untersuchungen zur angewandten Bodenbiologie, Band I. "Musterschmidt", Wissenschaftlicher Verlag, Göttingen. 179 pp., 3 colour pl., 96 fig., 3 diagr. 1954. 19.80 DM ($4.50 approx.)

Although Dr. Brauns has prepared this volume from the viewpoint of the forest zoologist, it will certainly appeal to a wide circle of entomologists for whom a knowledge of the habits of soil-inhabiting organisms is a basic necessity, and who, though not specialists, wish to undertake the identification of the dipterous larval forms most frequently encountered in the soil. For the latter purpose, the author has provided a great many excellent line drawings of whole larvae and of diagnostically-important details. These supplement a key to 52 families and subfamilies, with ninety pages of descriptions, biological information, and, in several cases, keys to genera and notes on individual species. Besides this systematic treatment, there is a section of 15 pages dealing with dipterous larvae in their general relation to soil biology, including methods for studying the soil profile, adaptations of larvae to the special environmental conditions, their seasonal activity, the density of larval populations and their role and importance relative to the other members of the biological community. Finally there is a general section on morphology of larval Diptera, also supported by carefully prepared drawings. The text appears to be well indexed, and there is a large bibliography, mostly of German titles. There are 44 pages of illustrations of larvae, eleven pages of habitat and biology photographs, two diagrams of seasonal activity and interrelations with other organisms, and three colour plates.

This book makes no claim to comparison with the recently-completed monumental work on larval Diptera by Hennig, but, unlike the latter, its price is within the means of most individual workers. It is a volume deserving of a place on the reference shelves of many field laboratories in Canada. A companion volume by Dr. Brauns on dipterous pupae has already been announced. If of the same high standard of execution as the present work, it should have an equally favourable reception.

G. E. SHEWELL

Studies on a Direct Feeding Method for Use in Bioassay of Insecticide Residues[1]

By R. W. Fisher and B. N. Smallman

INTRODUCTION

The absence of adequate chemical and enzymological micro-methods for the estimation of residues of the chlorinated hydrocarbon insecticides increases the need for reliable bioassay methods. The purpose of the work reported below was an investigation of the influences of cultural and testing techniques on the sensitivity and dependability of the toxicological response of the fruit fly, *Drosophila melanogaster*.

MATERIALS AND METHODS

Rearing

Drosophila melanogaster was reared on canned custard pumpkin using a modification of Bartlett's Method (1). The quality of the pumpkin was critical; dry, dark pumpkin was excessively susceptible to mould, but a moist, light yellow pumpkin was less likely to become mouldy and gave more consistent results. Sixty-five g. of pumpkin, 0.7 g. of cellucotton, and 1.5 g. dried Brewer's yeast were mascerated until smooth in a Waring type blendor and placed in the bottom of a pint milk bottle. Twenty-four females and eight males (4 days old) were introduced for 24 hours to oviposit. On the third day the bottle was lined with paper towelling on which the larvae then pupated. Bottles were sealed with a piece of paper towelling secured by a rubber band and kept at a temperature of 78°F. Pupation was completed by the fifth day and flies began emerging on the eighth day. Adults were aspirated from the bottle when one day old, and were kept in one quart seal rite container cages for stocks or for testing. One end of the container was closed with Orlon screen, the other with ½" plywood. An injection type feeding trough containing a mixture of pumpkin, molasses and yeast was inserted through the wooden end and refilled daily without the flies escaping from the cage.

A satisfactory probit line can be obtained with as few as 250 flies; therefore it seemed preferable to rear *Drosophila* in small cultures and to set up multiple batches for larger numbers. Also, since the larvae are quickly killed or retarded by the presence of moulds, any culture containing a trace of mould could be discarded if a number of small cultures were available. Pint bottles proved the most satisfactory rearing units.

Testing

Aldrin was used as the test insecticide throughout this study. Water suspensions were prepared from a 0.05% acetone solution of aldrin and all concentrations of toxicant in pumpkin were derived from these water suspensions. Fresh, canned custard pumpkin plus the toxicant was mascerated in a Waring blendor for one minute. Two g. of this treated tissue were then spread evenly along a ¾" x 5" strip of filter paper in a 1" x 6" test tube. A number of flies were then placed in the tube and the tube firmly stoppered with absorbent cotton. The tube was placed horizontally with the filter paper forming a roof. Moisture condensed on the glass, and the weakened, badly affected flies became trapped on the wet glass. All flies dead or trapped at 20 or 24 hours were recorded as dead; percent mortality reflected the effectiveness of the toxicant. Except where definite sex ratios were required, flies were allowed to enter the test tubes voluntarily without the use of anaesthetics.

[1]Contribution No. 42, Science Service Laboratory, Canada Department of Agriculture, London, Ontario.

Two types of experiments were conducted. In the first, the effects of variables such as age, sex, and numbers of flies were assessed by the mortality resulting from exposure to a range of concentrations of aldrin in custard pumpkin. In the second type of experiment, the residue of toxicant in a "sample" of treated plant material was estimated by comparison with a standard made up with the same plant material.

To test the accuracy and sensitivity of the method, a standard was prepared by adding a water suspension of aldrin to pumpkin which was then serially diluted with further known weights of pumpkin. This standard was then compared to a simulated "unknown" prepared in exactly the same way, except that a small "residue" of aldrin was added initially. In this way, the "residue" was serially diluted by the same factor as the standard. The effect of superimposing the "residue" upon a standard dilution series was to raise the mortality figures to the region of the 50% point where comparisons are most significant. The serial dilution of the "residue" as well as the standard provides a regression line parallel to the standard, and so comparisons can be made at any level on the line. This method differs from that of Sun and Sun (3) wherein one dosage is added to the residue-containing tissue and the resulting mortality plotted on a standard line. The residue there is the difference between the standard and the unknown plus standard.

Statistical

Logarithmic probability paper was used to plot mortality data, and the short method of Litchfield and Wilcoxon (2) was used for the statistical analyses. In plotting the results, the mortalities for the "unknown" were plotted at the same concentrations as for the standard. The "residue" in the unknown increased the mortality above that for the corresponding standard concentration so that the probit line for the unknown lay above the line for the standard.

Since the "residue" was serially diluted, the lines should be parallel, enabling the "residue" in the unknown to be calculated from the horizontal difference between the lines at any one point. When the lines satisfied the test for parallelism, a potency ratio was calculated to give a more accurate value for the residue.

RESULTS

Effect of Rearing Procedures

(a) Effect of medium on development: The presence of cellucotton appears to improve the pumpkin medium by stiffening it and permitting the larvae to feed more extensively. When the larvae had utilized all the nutrients from the upper quarter inch of medium, they were forced to burrow deeper. However, a larva cannot breathe through its posterior spiracles if submerged in moist tissue; so large numbers are forced to cooperate in burrowing at one location, thereby forming a cavity in the pumpkin with their posterior ends. But many were left undernourished and were delayed in pupating.

Thus in one experiment 33 females on the pumpkin medium produced a total progeny of 370, the mean weight of the males being 0.83 mg. and of the females, 1.02 mg. On the cellucotton-pumpkin medium, under parallel conditions, 33 females gave 720 offspring, of which the males averaged 0.80 mg. and the females 1.16 mg. The cellucotton, then, supplied the necessary stiffening matrix for the soft, moist pumpkin.

(b) Effect of age of breeding stock: Figure 1 shows that *Drosophila* females have a definite oviposition cycle, with egg production rising linearly to a peak at four days followed by a smaller peak at six days. This finding led to the use of 4-day old females throughout for rearing test insects. Investigations were not

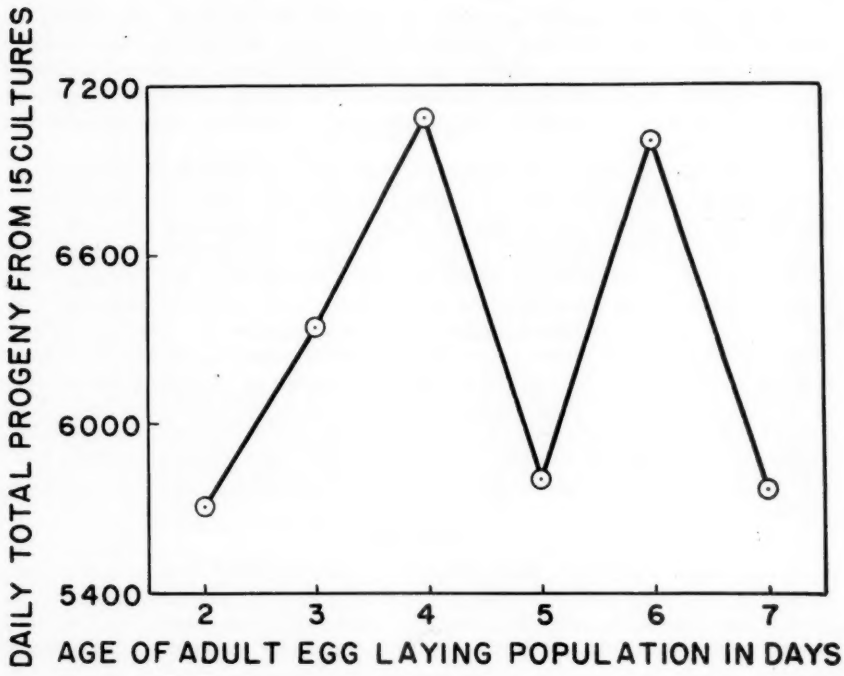

Figure 1

carried past the seventh day because the vitality of the males decreased after the fourth day.

(c) Effect of numbers of parent females: Figure 2 shows that the number of progeny produced tends to increase linearly as the number of females increases. As the number of progeny increases, the mean weight of the resultant adults decreases; up to 45 females per bottle may be used before the weight of progeny adults becomes too low for practical use. Obviously a gram of medium can

TABLE I
Effect of Males on Oviposition by Females

Number of females in the culture unit	Total progeny using female to male ratios:		
	3:0	3:1	3:3
18	2116	2225	2204
21	2561	2241	2461
24	2623	2774	3004
27	2928	3394	3497

A summation of data from 6 days' rearing, from 6 separate cultures each day containing parent flies 2, 3, 4, 5, 6 and 7 days old, respectively.

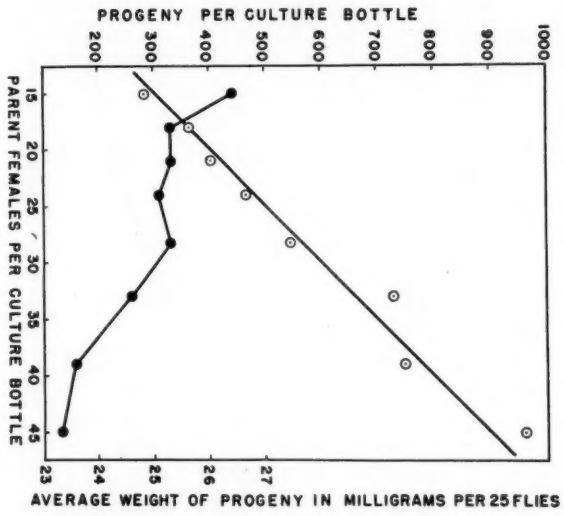

Figure 2

support only a definite number of developing larvae. Too few larvae in the medium fail to eat sufficient to prevent contamination by moulds while too many cause starvation of late-hatching larvae with a consequent wide range of pupal sizes and of pupation dates.

(d) Effect of ratio of males to females in breeding stock: An experiment was designed to show the effect of the presence of males in the culture jar while the females were laying. Table 1 shows that the presence of males tended to increase the number of progeny. This tendency is most pronounced when the number of females is greater than 21 per bottle. This finding, coupled with the finding that overcrowding leads to a decrease in weight, led to the choice of a ratio of 24 females to 8 males in standard cultures.

Effect of Testing Procedures

(a) Effect of age of test insects on susceptibility: A large culture of newly emerged flies was divided into four equal lots and one lot tested on each of four consecutive days. The results are shown in Figure 3. The Chi^2 value indicates the degree of heterogeneity in the response of the flies to the toxicant. The regression lines of probit mortality on Log. concentration of the 2-day and 4-day old flies are steeper than those of 1- and 3-day old flies, indicating a greater uniformity in their response to the toxicant.

The reasons for this variation with age were not investigated. It should be pointed out, however, that the 1-day old group included some newly-emerged flies and some heterogeneity might be expected in this group. Although good lines were obtained with both 2-day and 4-day old flies, only 2-day old flies were used in this study. The use of this age group had the additional advantage that handling was reduced and the males were still in good condition.

(b) Effect of sex ratio of test insects on mortality: Table 2 shows that males are considerably more susceptible to aldrin than females, as indicated by the decrease in L.D. 50 as the ratio of males to females increases. The table also shows that the uniformity of response to the insecticide is greatest when the sex

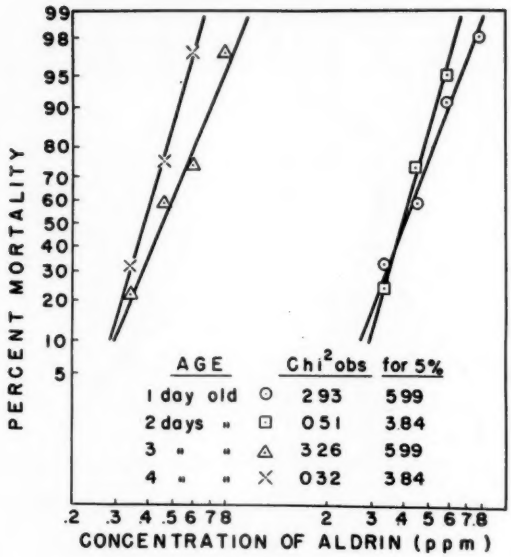

Figure 3

ratio is about 50:50; the Chi² value tends to increase as the sex ratio is altered to favour either males or females.

(c) Effect of sex ratio of parent stocks on susceptibility of progeny: Rearing units were set up with 3 different ratios of 4-day old males and females: 21 females and 21 males, 21 females and 7 males, and 21 females. The sexes had been together until the fourth day. Progeny were tested when two days old. Table 3 shows that there is no significant difference between the L.D. 50 values for the three groups.

(d) Effect of numbers of test flies per unit of treated pumpkin: When the number of flies per unit of treated material exceeds a certain level, the normal dosage–mortality response becomes more and more difficult to obtain. It can be seen from Table 4 that the Chi² value increases with the number of flies used per tube. As few as eight or ten per replicate give excellent regression lines. With higher numbers of flies the Chi² value increases rapidly, and usable readings

TABLE II
Effect of Male : Female Ratio on Mortality

No. of Females	No. of Males	L.D. 50	Calculated Chi²	Chi² for 5% level of significance
20	0	0.30	3.58	9.49
15	5	0.29	3.73	9.49
10	10	0.23	1.91	9.49
5	15	0.23	1.04	7.82
0	20	0.22	5.35	5.99

TABLE III
Effect of Sex Ratio of Parent Stocks on Susceptibility of Progeny

Sex ratio	21 ♀ :21 ♂	21 ♀ :7 ♂	21 ♀ :0 ♂
L.D. 50 (ppm.)	0.197	0.22	0 22

(L.D. 50's do not differ significantly)

between 16% and 84% become increasingly difficult to obtain. Figure 4 indicates that when the 30 flies per dosage are confined in one tube rather than divided into three lots of ten, the L.D. 50 increases from 0.23 to 0.28 ppm., the slope is lower and the Chi^2 value somewhat higher. There is, therefore, a maximum number of flies that can be exposed to a unit of treated tissue. When the number reaches 18 to 20 flies per tube, the crowding effect approaches that indicated in Figure 4, and the quantity of insecticide rather than the concentration becomes critical. It is obviously depleted rapidly by large numbers of flies, leaving the majority with a sub-lethal dose. Consequently, the mortalities are restricted to the lower portion of the line, i.e., below the 50% point.

(e) Advantage of replication: The use of three tubes per dosage permits the total number of flies per dosage to be increased without encountering the decrease in mortality due to overcrowding (Figure 4). Table 5 also shows that 5 replicates of 15 flies are superior to 3 in estimating a known residue in the pumpkin, especially where the flies are introduced alive from a darkened holding flask without an anaesthetic.

(f) Variability of sex ratio of test flies emerging from a holding chamber: Test flies were placed in a darkened chamber and attracted by light through a small glass exit into the test tubes. A count of the sexes revealed that in tubes containing 10 flies the ratio of males to females varied from 0:10 to 7:3. In the tubes with 30 flies the ratio varied from 17:13 to 22:8. So flies emerging from a darkened holding flask do so in groups of one sex or the other; consequently, if they are introduced into the test tubes as they emerge, the sex ratio for the different dosages will vary considerably and so give a biased mortality response. The Chi^2 value for the line will then be high unless enough replications are taken to

TABLE IV
Effect of No. of Test Flies per Unit Treated Tissue

No. flies per tube	Chi^2 calculated*
8	0.176
10	0.126
12	1.890
14	3.970
16	1.01
18	4.98
20	12.90

* Chi^2 for 5% level of significance = 5.99.

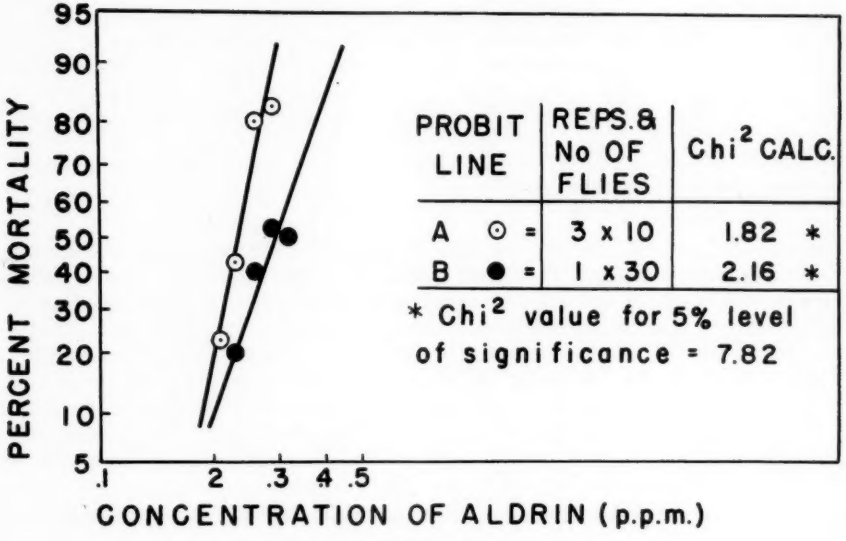

Figure 4

bring the sexes closer to the 50:50 ratio. For this reason, the flies were counted and sexed under ether and then placed in the tubes.

Estimation of Residues

(a) Bioassay of simulated residues: Table 5 shows the accuracy with which the method yields estimates of known "residues" of aldrin under various conditions. Five replicates of 15 unsexed flies gave the most accurate result, but three replicates of ten sexed flies proved satisfactory and involved much less work. In all trials but one the estimate was somewhat higher than the residue added. This discrepancy may be due to the movement of the toxicant to the surface layer of the pumpkin as the flies remove water from it.

(b) Bioassay of an unknown residue: Two samples of canned applesauce from apple trees sprayed with dieldrin and from non-sprayed apple trees were assayed by the above method except that 3 lots of 30 flies (not anaesthetized) were used

TABLE V
Estimates of Known Residues Under Various Experimental Conditions

"Residue" added (p.p.m.)	No. of flies per dosage	Estimated residue (p.p.m.)
0.1	* 2 replicates of 30	0.14 ± 0.03
0.05	* 3 replicates of 15	0.10 ± 0.03
0.05	* 5 replicates of 15	0.05 ± 0.03
0.05	† 3 replicates of 10 (5 males, 5 females)	0.08 ± 0.02

* Flies introduced from darkened flask to tubes by phototaxis.
† Flies anaesthetized with ether and introduced to tubes with a camel's hair brush.

for each dosage. Though the large numbers of flies undoubtedly reduced the sensitivity of the test, the assay revealed a residue of 0.36 ± 0.03 ppm. in one sample and 0.18 ± 0.02 ppm. in the other. From information on the dosages applied to the trees, these results are in the correct order. This example is given to show the sensitivity of the method applied to plant material containing residues of dieldrin.

SUMMARY

A method is described for rearing *Drosophila melanogaster* adults of uniform vigour and susceptibility to insecticides for use in bioassay procedures. The effects on susceptibility of the following variables were tested in order to arrive at the most reliable conditions for the bioassay: age of test insects, sex ratio of test insects, sex ratio of parent flies, numbers of test flies per unit of treated tissue, anaesthesia and replication of numbers at each dosage.

The bioassay procedure is based on the direct feeding by the flies on the residue-containing plant material without requiring previous extraction of the toxicant.

The statistical analysis requires that the "unknown" be serially diluted so that the residue is likewise diluted and the "standard" and "unknown" probit lines are parallel. For rapid estimation the values of the residue can then be read directly from the graph. The results show that valid estimations of aldrin may be made at levels of 0.05 ppm.

A sample bioassay of dieldrin in applesauce, and several bioassays of known quantities of aldrin added to pumpkin are presented.

ACKNOWLEDGMENTS

The authors wish to thank Mrs. I. Christie, Mr. Florian Jursic and Miss Eva Zwanzig for assistance in rearing the flies and in carrying out some of the tests, and Dr. H. Martin for his helpful criticism of the paper.

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(Received November 16, 1954)

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Some Aspects of the Biology and Dispersal of the Pine Tortoise Scale, *Toumeyella numismaticum* (Pettit and McDaniel) (Homoptera: Coccidae)[1]

By F. B. Rabkin[2] and R. R. Lejeune[3]
Forest Biology Laboratory, Winnipeg, Canada

FOREWORD

The senior author conducted this investigation during 1937 and 1938 in the Sandilands Forest Reserve, Manitoba. The results were presented in an unpublished report (Rabkin, 1938). Owing to the current importance of this insect in Manitoba and the Lake States of the United States, it was considered advisable to publish those aspects of the work relating to life history and dispersal. This was undertaken by the junior author.

INTRODUCTION

The insect studied is a soft scale. Specimens submitted to W. R. Richards, Entomology Division, Ottawa, in 1954, were identified as the pine tortoise scale, *Toumeyella numismaticum* (Pettit and McDaniel).

In general, the distribution of the pine soft scales coincides with the northern coniferous regions of the United States and Canada. The economic importance of these scales was first mentioned by L. O. Howard (1907). Studies of *T. numismaticum* have been carried out by Orr (1931), Pettit (1931) and others.

In the Sandilands Forest Reserve *T. numismaticum* attacks jack pine (*Pinus banksiana* Lamb.), Scots pine (*P. sylvestris* L.), and red pine (*P. resinosa* Ait.), in order of preference. The scale is most prevalent on young trees and may kill or severely damage young pines in plantations or natural stands. It has been a sporadic problem in the Reserve since 1935.

LIFE HISTORY OF *T. NUMISMATICUM*

Early Spring Activity

Scales are amongst the first insects to become active in the spring. At the beginning of the season, the female scale is wrinkled, deep brown to black, and appears to be dead. At this time it is about half grown. As development proceeds, the scale fills out, becomes more rounded, and the colour changes to reddish-brown. Beginning of development coincides with the swelling of the buds and the start of terminal growth of jack pine. This period is characterized by a copious secretion of honey-dew by the scales. In 1938, honey-dew was first noted on May 15. Where ants are not present to consume the secretion, it collects on the trees, forming the substrate for a conspicuous sooty fungus.

Maturation and Egg Development

At the beginning of spring activity, the area of the female scales averages about 5.5 sq. mm. Mature scales average 13 sq. mm. The mature insect is decidedly convex and broadly oval (Figure 1).
Dorsally, three longitudinal light-coloured bands converge cephalad and caudad. There are two or more rows of small circular depressions in the regions of the bands.

Egg development in the scales was well advanced by June 6 in 1938. At this stage of development most of the eggs are in the uterine envelope, but some are free in the body cavity. Embryonic stages of the developing nymphs can be

1Contribution No. 167, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.
2Officer, Forest Biology Laboratory, 1937 to 1942.
3Officer in Charge.

Fig. 1. Jack-pine twigs showing mature female scales and larvae of a coccinellid predator.

seen in the more advanced eggs, while undifferentiated eggs are present in the ovary. A few days after the eggs are liberated into the body cavity, the internal structures of the scale begin to lose their identity, and the body cavity becomes filled with a reddish-brown fluid. The developing eggs float in this fluid.

Nineteen mature or nearly mature scales were dissected to determine the number of ova per female. The number averaged 534, with the standard error of the mean $\pm$ 50[1]. The size of the scales averaged 13.1 sq. mm., with the standard error of the mean $\pm$ 0.67 sq. mm. There was a correlation between scale area and number of eggs present. The correlation was 0.881, which is significant beyond the .01 level.

Oviposition and Emergence

As far as could be determined, the process of oviposition consists of the extrusion of the almost fully developed egg from the genital aperture located in the posterior ventral region of the insect. Usually the eggs are extruded singly, but chains of three or four eggs have been observed. Shortly after extrusion, usually a few hours, the colour of the egg becomes lighter, and eclosion of the nymph takes place. Newly emerged nymphs spend up to a half day under the shell of the female scale before crawling away. As the nymphs emerge, the ventral space underneath the scale is filled with cast chorions.

Nymphal emergence was first noted in the field on June 21 and was general

1Orr (1931) obtained 1,524 ova from one mature female. This disparity may be caused by regional, seasonal, or host differences.

by June 23. Observations of six caged females showed that nymphs emerged from June 24 to July 4, with the majority emerging during the first three days.

Nymphal Feeding

Following the selection of a suitable site, the nymphs begin to feed. In 1938, feeding was general by July 7. Though some preference is shown for new growth, nymphs settle down anywhere on the branches and twigs.

On the first day of feeding, no external changes are evident. In the second day, a white powdery material appears at the outer ventral margins of the nymphs. Except for an increase in size, no further external changes occur up to the fourth or fifth day.

At this time, segmentation and nymphal markings are lost, and the insects assume the typical scale appearance. Growth progresses uniformly for about two weeks without visible sexual differentiation.

Following this two-week feeding period, various external changes can be observed. Males cease to grow laterally and begin to elongate, while females continue to grow uniformly. About three weeks after the beginning of feeding, the males are full grown and can be readily recognized by their clear, waxy covering (Figure 2). Females are still immature, and are convex, broadly oval in shape, resembling the mature scale.

Sex Ratios

The sexes may be readily distinguished by the last week of July. Random samples from infested trees were collected to determine general sex ratios and related data. A total of 9,168 scales were counted; of these 6,456 were alive. Data pertaining to the distribution of scales on the host tree and sex ratios are given in Table 1.

TABLE I
Sex Ratios and Related Data for Scale Counts

Location on tree	Average scales/ linear inch	Percentage dead	Ratio ♂ to ♀
Main stem	33.9	9.5	44:56
Branch	39.5	26.5	55:45
Twig	37	54	57:43

The table shows that the proportion of males to females tends to increase as the mortality rises, indicating a selective mortality of females. No consistent relation was found between population density and sex ratio, but it was observed that there are a lower proportion of females to males on severely infested trees suffering from the effects of scale attack.

Fertilization and Development

The first adult males emerged on August 3, and began to fly immediately. The adult is small, fragile, and has no mouth parts or alimentary system. The gonads occupy the entire abdominal cavity. Males rarely live more than two days in captivity.

Females are fertilized in the immature stage, which resembles the adult female except for size. Ventral segmentation is apparent and the mouth parts are well developed. The antennae and legs are greatly reduced and locomotor function is lost. Within a few hours after fertilization, the female begins to secrete honey-

Fig. 2. Male scales on a twig of jack pine.

dew. The female continues to develop well into the fall; secretion of honey-dew has been observed in late September.

DISPERSAL

Following emergence of nymphs from the eggs in late June and early July, experiments were carried out on factors contributing to dispersal. A knowledge of these factors is essential for following the course of scale infestations, and for planning control procedures. Various authors have suggested that birds, squirrels, ants, and other insects might be responsible for spreading nymphs. The senior author felt that animal agencies are only incidental and that wind and air currents might easily carry nymphs for appreciable distances, thereby starting new infestations. Such migratory activities could account for the patchy condition of the infestation in the Sandilands Forest Reserve in 1938.

Methods

Tanglefoot traps were placed in various parts of the Reserve to capture nymphs. A commercial preparation of tanglefoot was spread evenly on sheets of white bond paper, 8 by 10 inches. A 1-inch margin was left free for handling. The papers were tacked to boards of slightly larger dimension that had first been nailed to stakes 3, 6, and 9 feet high. In addition, similar traps were placed on top of an 80-foot fire-lookout tower.

After various periods of exposure, the papers were removed and the nymphs trapped in the tanglefoot were counted.

Under "Results" the term "trap-day" refers to one tanglefoot trap exposed for one day. The first traps were exposed on June 21 and the last trap was removed from the field on August 28, though the dates of exposure of individual traps varied considerably within this period.

Results

Table 2 summarizes the number of nymphs captured in traps in various locations in the Reserve.

TABLE II
Summary of Scale Nymphs Caught in Tanglefoot Traps

Location No.	Location of traps	No. of traps	No. of trap-days	Nymphs trapped	Nymphs per trap-day
1	Centre of heavily infested area	7	131	2,481	18.9
2	1925 seed plots in heavily infested area	7	124	2,231	18.0
3	Another point in heavily infested area	9	126	21,903	173.8
4	Opening in heavily infested area about ½ mile from nearest trees	4	84	107	1.3
5	Lightly infested, 2–3 miles removed from edge of severe infestation	13	553	1,503	2.7

In location 1, over half the nymphs were trapped during the first nine days of exposure. In location 2 the greatest number were also caught during the early part of the period.

Special interest attaches to results from traps exposed on an 80 foot fire-lookout tower, near the edge of a severe infestation. The tower is situated on a knoll, and the traps at the top of the tower would be about 100 feet above the surrounding country.

A number of traps were exposed at the top of the tower, and at the base about 3 feet above ground level. In 163 trap-days, 119 nymphs were caught at the top of the tower. At the base, 2,038 were captured in 130 trap-days.

About 99 per cent of the nymphs trapped in the experiments described were caught during the period June 21 to August 2.

An effort was made to determine if windborne migration is an accidental or deliberate process. Nymphs were difficult to dislodge from severely infested branches that were shaken vigorously. In another instance, traps were placed beneath infested trees and also 15 to 25 feet removed. There were no other scale-infested trees in the immediate vicinity. Traps 25 feet removed from the nearest tree caught about three times as many nymphs as those underneath trees.

However, these two observations should not be accepted as conclusive evidence that nymphs do not drop from the trees. In some instances many nymphs were seen on the ground beneath infested trees. Firm conclusions can only be based on more extensive studies and observations under a variety of conditions.

During these investigations it was observed that nymphs move about on trees on which they emerge, and from one tree to another where the branches intertwine. However, it is believed that few new trees are infested by this means of dispersal.

Discussion

In the experiments described in this section, it was demonstrated conclusively that large numbers of nymphs are distributed by air currents. The number distributed varies with the density of the stand, but the precise influence of stand density cannot be determined from the data available.

It was shown that nymphs can be carried for distances up to three miles but it is doubtful if many new infestations can be established by windborne dispersal much beyond a 3-mile radius from the edge of an infestation. In reviewing results of his own and other work, Wellington (1945) concluded that long-distance distribution of insects by wind usually may be neglected since it is an unsteady phenomenon, but that short-range, high- or low-altitude processes, produced by local topography, are of utmost significance economically.

No data are available on animal agents of migration. There is a strong possibility that birds, squirrels, and insects may transport nymphs from tree to tree and, in some cases, over a considerable distance. Locomotor migration by nymphs is probably limited to the tree on which they emerge or to adjacent trees where the branches intertwine.

SUMMARY

The scale studied was identified as the pine tortoise scale, *Toumeyella numismaticum* (Pettit and McD.). In Manitoba the insect attacks jack pine, Scots pine, and red pine in this order of preference. It is primarily a pest of seedlings and saplings.

The half-grown, fertilized females start development in the spring when the jack-pine buds begin to swell and terminal growth commences. The scales mature rapidly and egg development begins in early June. The number of ova per female averaged 534. Oviposition begins shortly after mid-June. Oviposition consists of the extrusion of almost fully developed eggs, singly or in short chains, from the genital aperture in the posterior ventral region of the insect. Newly emerged nymphs spend up to one-half day under the female scale before crawling away. Nymphal emergence takes place during late June and early July.

Following emergence, the nymphs undergo a period of dispersal, principally by means of wind and air currents. Some locomotor migration was also observed.

After finding a suitable host, the nymphs begin to feed. Following a two week feeding period, males and females begin to show external evidence of differentiation. Normally males and females occur in about equal numbers. Male scales are mature after three weeks of feeding. Adult males emerge in early August and fertilize the immature females, which continue development well into September.

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(Received November 16, 1954)

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A New Locality Record for the Termite in Ontario

By F. A. URQUHART*

In my paper "The Introduction of the Termite into Ontario" (*Can. Ent.*, No. 8, 1953) I stated that "insofar as records based on collected specimens are concerned, the termite, *Reticulitermes flavipes*, is to be found in no other part of eastern Canada, with the exception of Pelee Island (where this particular species has been present for many years)." I further stated that "it is forecast that it will continue to spread over the entire area of eastern Toronto including greater Toronto" and further that "its appearance in other parts of the Province is to be expected, and it will no doubt occur in isolated populations similar in pattern, but on a larger scale, to what has been witnessed in Toronto during the past fourteen years."

I wish, in this short paper, to record the existence of a permanent, and apparently isolated, population of *Reticulitermes flavipes*, in Kincardine, Bruce County, Ontario. The specimens, now contained in the collection of the Royal Ontario Museum, were collected by Mr. George Francis on September 4th, 1954, from beneath a pile of rubbish close to the railway station.

It is well within the realm of probability that this destructive insect pest will follow a pattern of population expansion in the Kincardine area similar to that which has been experienced in the Toronto area.

*Royal Ontario Museum of Zoology and Palaeontology.

O. I. S. Exchange

THE RUNGE PRESS LIMITED, OTTAWA
Mailed: Friday, January 7, 1955